

2008

# Vegetation change over time in naturally-regenerating Coast Redwood communities

Kristin K. Hageseth  
*San Jose State University*

Follow this and additional works at: [https://scholarworks.sjsu.edu/etd\\_theses](https://scholarworks.sjsu.edu/etd_theses)

---

## Recommended Citation

Hageseth, Kristin K., "Vegetation change over time in naturally-regenerating Coast Redwood communities" (2008). *Master's Theses*. 3574.

DOI: <https://doi.org/10.31979/etd.wsuc-k76x>

[https://scholarworks.sjsu.edu/etd\\_theses/3574](https://scholarworks.sjsu.edu/etd_theses/3574)

This Thesis is brought to you for free and open access by the Master's Theses and Graduate Research at SJSU ScholarWorks. It has been accepted for inclusion in Master's Theses by an authorized administrator of SJSU ScholarWorks. For more information, please contact [scholarworks@sjsu.edu](mailto:scholarworks@sjsu.edu).

VEGETATION CHANGE OVER TIME IN  
NATURALLY-REGENERATING  
COAST REDWOOD COMMUNITIES

A Thesis

Presented to

The Faculty of the Department of Environmental Studies

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Kristin K. Hageseth

August 2008

UMI Number: 1459693

## INFORMATION TO USERS

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleed-through, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

**UMI**<sup>®</sup>

---

UMI Microform 1459693

Copyright 2008 by ProQuest LLC.

All rights reserved. This microform edition is protected against unauthorized copying under Title 17, United States Code.

ProQuest LLC  
789 E. Eisenhower Parkway  
PO Box 1346  
Ann Arbor, MI 48106-1346

© 2008

Kristin Hageseth

ALL RIGHTS RESERVED

**APPROVED FOR THE DEPARTMENT OF  
ENVIRONMENTAL STUDIES**



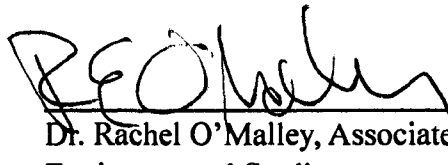
---

Dr. Will Russell, Committee Chair, Department of Environmental  
Studies



---

Dr. Lynne Trulio, Professor, Department of Environmental Studies



---

Dr. Rachel O'Malley, Associate Professor, Department of  
Environmental Studies

**APPROVED FOR THE UNIVERSITY**



## ABSTRACT

### VEGETATION CHANGE OVER TIME IN NATURALLY-REGENERATING COAST REDWOOD COMMUNITIES

by Kristin K. Hageseth

Less than 5% of the Pacific coast's original old-growth coast redwood (*Sequoia sempervirens*) forests remain and regenerating redwood forests are subject to timber harvest. This research measured native species recovery in stands of different ages compared to old-growth stands in redwood forests in Mendocino County, California. Dominance, density, frequency, and diversity of overstory and understory species were collected over the summer flowering season of 2007 in the Big River Watershed and surrounding regions. ANOVA and regression analyses demonstrated that several stand and understory parameters, including tree density, canopy cover, and understory richness, approached old-growth levels without human intervention. Exotic species were less common in older stands, allowing native plant species to dominate. Whether natives can out-compete more recently introduced non-natives in younger stands requires further study. These findings suggest restoration within regenerating redwood communities of the Big River Watershed may benefit from allowing natural succession.

## Acknowledgements

I thank my committee members, Dr. Will Russell, Dr. Lynne Trulio, and Dr. Rachel O'Malley for their limitless advice and direction in many aspects of my education and thesis writing. Dr. Shannon Bros of the biology department of San Jose State was also an invaluable resource.

I would also like to thank Save-the-Redwoods-League, the College of Social Sciences at San Jose State, and Cal Winslow of the Mendocino Institute for providing financial assistance as well as California State Parks for providing permits and access. I thank the staff at the Mendocino District State Parks Office, especially Renee Pasquinelli and Bill Maslach for their pleasant demeanor and for facilitating access to remote locations within the Big River Watershed. I am also very grateful for Helene Chalfin at Jughandle Creek Farm and Nature Center in Caspar for providing lodging throughout my research.

The California Department of Forestry and Fire Protection, particularly Marc Jameson, Rob Rutland, and Lynn Webb offered personal knowledge of the harvest history within Jackson State Demonstration Forest. Rob Rutland of the Santa Rosa CDF office deserves additional recognition as he provided the initial harvest history data for the entire Big River Watershed, making this study possible.

Countless other professionals aided this study including Greg Giusti of the University of California Cooperative Extension, James Bernard and Matt Coleman of the Mendocino Land Trust, Dan Porter of Save-the-Redwoods-League, Sarah Billing and

Doris Schoenhoff of the Mendocino Redwood Company, and Jenny Griffin at the Mendocino Land Trust. I am thankful for all their help.

I owe much of the success of this project to my faithful field assistants who traversed many backcountry areas of the Big River Watershed and beyond. These assistants included Zach Michels, Suzie Woolhouse, Matt Stender, Ariel Rivers, Ky Russell, Mike Tkalevic, Scott Morford, Dave Hageseth, and Carlos Cornejo. My primary field assistant, Suzie Woolhouse, cleared many paths and added enthusiasm during the arduous hiking. My husband, Zach Michels, offered many hours of his time in the field and out of the field, especially involving GIS query and analysis. His support and encouragement were invaluable throughout this project. I would also like to give special thanks to my thesis chair and dear friend, Will Russell, for his enduring passion for forests, education, and the environment. I am very grateful for his guidance.

Most importantly, I am very thankful for the love and support of my parents, family, and friends during the evolution of this project and my studies at San Jose State. These individuals were truly an integral part of my education and I am deeply appreciative of all their help.

Lastly, I would like to thank the redwood trees. They allowed much disturbance to their natural environment throughout my research and they also provided support in times of desperate climbing. I hope in the future they are less agitated by research.



## Table of Contents

List of Figures.....	viii
List of Tables.....	xi
Introduction.....	1
Background.....	3
<i>Characteristics of Sequoia sempervirens</i> .....	3
<i>Succession Theory and Coast Redwood Forests</i> .....	7
<i>Diversity Theory</i> .....	14
<i>Restoration Concepts</i> .....	15
Related Research.....	18
<i>Succession of Dominant Tree Species in Redwood Forests</i> .....	18
<i>Succession of Understory Vegetation in Non-Redwood Forests</i> .....	24
<i>Succession of Understory Vegetation in Redwood Forests</i> .....	27
Research Objectives.....	31
Methods.....	32
<i>Study Area</i> .....	32
<i>Study Design</i> .....	33
<i>Analytical Methods</i> .....	40
Results.....	44
<i>Overall Relationships</i> .....	44
<i>Stand Parameters</i> .....	46
<i>Tree Species Parameters</i> .....	52
<i>Understory Parameters</i> .....	64
<i>Understory Species Parameters</i> .....	71
Discussion.....	80
<i>Stand Dynamics</i> .....	80
<i>Understory Dynamics</i> .....	86
Recommendations.....	92
References.....	96
Appendix A. Non-response variable data and dominant canopy species.....	105
Appendix B. Species list.....	115
Appendix C. Summary of concluding results.....	122

## List of Figures

<i>Figure 1.</i> Timber harvest history, Big River Watershed, Mendocino County.....	35
<i>Figure 2.</i> Regenerating sample sites, Big River Watershed, Mendocino County.....	36
<i>Figure 3.</i> Regenerating stands and old-growth stands, Mendocino County.....	38
<i>Figure 4.</i> Principal components analysis with component loadings characterizing regenerating redwood stands of the Big River Watershed.....	45
<i>Figure 5.</i> One-Way ANOVA between mean tree density and age class in regenerating and old-growth forests.....	47
<i>Figure 6.</i> One-Way ANOVA between mean canopy cover and age class in regenerating and old-growth forests.....	48
<i>Figure 7.</i> One-Way ANOVA between mean tree species richness and age class in regenerating and old-growth forests.....	49
<i>Figure 8.</i> One-Way ANOVA between mean Shannon-Weiner Diversity Index of tree species and age class in regenerating and old-growth forests.....	50
<i>Figure 9.</i> One-Way ANOVA between mean species richness and age class in regenerating and old-growth forests.....	51
<i>Figure 10.</i> One-Way ANOVA between mean dominance and age class in regenerating and old-growth forests.....	53
<i>Figure 11.</i> One-Way ANOVA between mean <i>Sequoia sempervirens</i> dominance and age class in regenerating and old-growth forests.....	54
<i>Figure 12.</i> One-Way ANOVA between mean <i>P. menziesii</i> var. <i>menziesii</i> dominance and age class in regenerating and old-growth forests.....	55
<i>Figure 13.</i> One-Way ANOVA between mean <i>Lithocarpus densiflorus</i> dominance and age class in regenerating and old-growth forests.....	56
<i>Figure 14.</i> One-Way ANOVA between mean <i>Tsuga heterophylla</i> dominance and age class in regenerating and old-growth forests.....	57
<i>Figure 15.</i> One-Way ANOVA between mean <i>Sequoia sempervirens</i> importance and age class in regenerating and old-growth forests.....	59

<i>Figure 16.</i> One-Way ANOVA between mean <i>Tsuga heterophylla</i> importance and age class in regenerating and old-growth forests.....	60
<i>Figure 17.</i> One-Way ANOVA between mean <i>Umbellularia californica</i> importance and age class in regenerating and old-growth forests.....	61
<i>Figure 18.</i> One-Way ANOVA between mean <i>Lithocarpus densiflorus</i> importance and age class in regenerating and old-growth forests.....	62
<i>Figure 19.</i> One-Way ANOVA between mean <i>Abies grandis</i> importance and age class in regenerating and old-growth forests.....	63
<i>Figure 20.</i> One-Way ANOVA between mean understory species cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	65
<i>Figure 21.</i> One-Way ANOVA between mean herbaceous species cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	66
<i>Figure 22.</i> One-Way ANOVA between mean Shannon-Weiner Diversity Index of understory species and age class in regenerating and old-growth forests .....	67
<i>Figure 23.</i> One-Way ANOVA between mean understory species richness and age class in regenerating and old-growth forests.....	68
<i>Figure 24.</i> One-Way ANOVA between mean understory species evenness and age class in regenerating and old-growth forests.....	69
<i>Figure 25.</i> One-Way ANOVA between mean exotic species cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	70
<i>Figure 26.</i> One-Way ANOVA between mean <i>Trillium ovatum</i> cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	72
<i>Figure 27.</i> One-Way ANOVA between mean <i>Tiarella trifoliata</i> var. <i>unifoliata</i> cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	73
<i>Figure 28.</i> One-Way ANOVA between mean <i>Viola sempervirens</i> cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	74
<i>Figure 29.</i> One-Way ANOVA between mean <i>Oxalis oregana</i> cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	75
<i>Figure 30.</i> One-Way ANOVA between mean <i>Gaultheria shallon</i> cover (m <sup>2</sup> /hectare) and age class in regenerating and old-growth forests.....	76

*Figure 31.* One-Way ANOVA between mean *Rhododendron macrophyllum* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.....77

*Figure 32.* One-Way ANOVA between mean *Toxicodendron diversilobum* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.....78

## List of Tables

Table 1. Mean tree species density post hoc comparisons between age classes.....	47
Table 2. Mean canopy cover post hoc comparisons between age classes.....	48
Table 3. Mean tree species richness post hoc comparisons between age classes.....	49
Table 4. Mean Shannon-Weiner Diversity Index of tree species post hoc comparisons .....	50
Table 5. Mean species richness post hoc comparisons between age classes.....	51
Table 6. Mean tree species dominance post hoc comparisons between age classes.....	53
Table 7. Mean <i>S. sempervirens</i> dominance post hoc comparisons between age classes .....	54
Table 8. Mean <i>Pseudotsuga menziesii</i> var. <i>menziesii</i> dominance post hoc comparisons .....	55
Table 9. Mean <i>L. densiflorus</i> dominance post hoc comparisons between age classes .....	56
Table 10. Mean <i>T. heterophylla</i> dominance post hoc comparisons between age classes .....	57
Table 11. Mean <i>S. sempervirens</i> importance post hoc comparisons between age classes.....	59
Table 12. Mean <i>T. heterophylla</i> importance post hoc comparisons between age classes.....	60
Table 13. Mean <i>U. californica</i> importance post hoc comparisons between age classes .....	61
Table 14. Mean <i>L. densiflorus</i> importance post hoc comparisons between age classes .....	62
Table 15. Mean <i>Abies grandis</i> importance post hoc comparisons between age classes...	63
Table 16. Mean understory species cover post hoc comparisons between age classes.....	65
Table 17. Mean herbaceous species cover post hoc comparisons between age classes....	66

Table 18. Mean Shannon-Weiner Diversity Index of understory post hoc comparisons .....	67
Table 19. Mean understory species richness post hoc comparisons between age classes.....	68
Table 20. Mean understory species evenness post hoc comparisons between age classes.....	69
Table 21. Mean exotic species cover post hoc comparisons between age classes.....	70
Table 22. Mean <i>Trillium ovatum</i> cover post hoc comparisons between age classes.....	72
Table 23. Mean <i>T. trifoliata</i> var. <i>unifoliata</i> cover post hoc comparisons between ages .....	73
Table 24. Mean <i>Viola sempervirens</i> cover post hoc comparisons between age classes....	74
Table 25. Mean <i>Oxalis oregana</i> cover post hoc comparisons between age classes .....	75
Table 26. Mean <i>Gaultheria shallon</i> cover post hoc comparisons between age classes....	76
Table 27. Mean <i>R. macrophyllum</i> cover post hoc comparisons between age classes.....	77
Table 28. Mean <i>T. diversilobum</i> cover post hoc comparisons between age classes.....	78

## Introduction

Habitat destruction is a major cause of biodiversity loss worldwide. Coast redwood (*Sequoia sempervirens*) forests have suffered tremendous biodiversity loss from human disturbances, specifically timber harvesting. After European settlement, intensive logging destroyed more than 95% of original old-growth redwood forests (Noss, 2000; U.S. Fish & Wildlife Service, 1997). As a result, according to the U.S. Fish and Wildlife Service a number of species that depend on old-growth forests are currently endangered, including the northern spotted owl (*Strix occidentalis caurina*) and the marbled murrelet (*Brachyramphus marmoratus*). The health of aquatic species, such as salmonids, also depends on the condition of the adjacent vegetative community. Remaining redwood forests are vulnerable communities due to habitat loss from wood extraction and harvesting.

Redwood as a timber product is extremely profitable and pervasive. Previous research focuses primarily on the production and regenerative nature of *Sequoia sempervirens* if harvested (Conrad, 1997; Fritz, 1945; Veirs, 1996). Previous studies do not assess timber harvesting impacts on the plant community development as a whole (Busing & Fujimori, 2005; Lindquist, 2004a, 2004b; Oliver, Lindquist, & Strothmann, 1994). Since the Forest Practice Act of 1973, a Timber Harvest Plan must be completed before harvest may take place (M. Jameson, personal communication, April 10, 2007). Yet, substantial portions of regenerating second-growth forests are still unprotected from selective harvest, or thinning.

Harvest practices can negatively impact forest communities. The removal of canopy species exposes the forest floor to increased levels of solar radiation (Rivas-Ederer & Kjeldsen, 1998; Russell & Jones, 2001), which opportunistic and exotic species easily invade (Rivas-Ederer & Kjeldsen). Logging practices alter soil conditions (Stone & Wallace, 1998) through compaction (Corns, 1988), and reduce nitrogen levels in previous logged stands (Jussy, Ranger, Bienaime, & Dambrine, 2004) particularly near skid roads (Ebrecht & Schmidt, 2003). Restoration involving active management or thinning may have damaging effects on redwood forest communities.

Appropriate restoration methods for recovering second-growth coast redwood communities are imperative in order to recover rare species, retain biodiversity, and develop old-growth characteristics. Forests are the result of complex relationships interacting at different levels of the community, which may change after a disturbance. However, the impact of timber harvesting on the complete plant communities in regenerating second-growth coast redwood forests has not been adequately addressed.

This research is the first to evaluate clearcut logging effects on the entire redwood forest community. The study took place in the central range of California within the Big River Watershed of Mendocino County. This project will help restoration managers, land trust organizations, and State and National Parks by providing information on the rates at which redwood communities naturally regenerate after clearcut harvest. The data from this study can be directly used in designing restoration projects to effectively restore second-growth redwood communities and aid ecosystem recovery.



## Background

### *Characteristics of Sequoia sempervirens*

Climatic changes over the late Pleistocene and early Holocene limited the range of redwood forests to a small strip of coastal land ranging from Curry County, Oregon to Monterey County, California (Hickman, 1993; McBride, 1977; Roy, 1966). *Sequoia sempervirens* are the tallest trees in the world and second to largest in biomass after *Sequoiadendron giganteum* (Veirs, 1996). Redwoods may grow from sea level to 3200 feet (Hickman) although they do not usually occur immediately next to the shore, due to the salty ocean spray and strong winds (Barbour et al., 2001; Roy). Redwoods give way to other species as elevation, moisture, and slope increases, preferring alluvial flats (Roy) and areas with high amounts of fog (Burgess & Dawson, 2004). Redwood trees also have strict temperature requirements, depending on adaptations to the local climate, and maximum growth occurs between 59° and 66° Fahrenheit (Roy). *Sequoia sempervirens* is a long-lived species, maturing between 400 and 500 years (Hickman) and capable of reaching ages of 2,200 years or more (Fritz, 1957). High genetic variation exists within *Sequoia sempervirens*. Redwoods are hexaploid, a rare condition among conifers, resulting in six sets of eleven chromosomes each (Barbour et al.). The variability within the species produces different colors of foliage, growth rates, growth patterns, and tolerance levels (Barbour, et al.).

Redwoods have the unique ability among conifers to reproduce through vegetative sprouting. Basal sprouting usually occurs when accumulated stem cells in the

lignotubers, or burls, at the base of the trees sprout after a hormonal response to a disturbance, releasing the dormant buds (Barbour et al., 2001; McBride, 1977; Sawyer, Sillett, Libby, et al., 2000). Redwood trees generate growth regulators that normally suppress bud sprouting unless the tree is damaged (Barbour et al.). Clonal sprouting patterns vary in spatial distribution but may include concentric circles ("fairy rings" or "sprouting rings"), figure-eight patterns, or elaborate chains connected through widespread underground root systems (Douhovnikoff, Cheng, & Dodd, 2004). The cloning ability is rare among conifers, although extremely prevalent in California nutmeg (*Torreya californica*) and moderately vigorous in Pacific yew (*Taxus brevifolia*) (Hickman, 1993). Sprouting in redwood trees is not limited to the burls and may occur along sides or tops of stumps, as well as along the length of the whole trunk (Barbour et al.; Roy, 1966). Clonal sprouting is the primary method of reproduction for redwoods (Douhovnikoff et al.) due to the low success rate of redwood seed establishment (Barbour et al.; McBride).

Redwood trees are extremely resilient to disturbances, such as fire, insect infestation, disease, and flooding (Barbour et al., 2001; McBride, 1977; Veirs, 1996). Several factors contribute to the high resistance level of redwood trees. Redwoods have extremely thick bark, which insulate and defend the cambium layer against disease and fire damage (Barbour et al.). The thick, fibrous bark of redwood trees is also a poor conductor of heat and does not burn efficiently (Barbour et al.). If a redwood does encounter fire, the central portion (heartwood) of the tree may burn, creating a "goose

pen," leaving the living tissue layer intact (Sawyer, Sillett, Libby, et al., 2000).

Redwoods with large goose pens are still capable of activating dormant buds, sprouting new shoots (Sawyer, Sillett, Libby, et al.). Young redwood trees are more susceptible to fire damage, due to the relatively thin bark of trees less than twenty years old (McBride).

Redwoods contain high levels of tannins and phenolics in the wood cells, which are extremely difficult for organisms to digest (Barbour et al., 2001). These chemicals protect the living tissue of the tree from insect infestation or pathogens. Redwoods also rely on a complex network of root systems that involve fungal associations (Sawyer, Sillett, Libby, et al., 2000). Since redwoods do not have a taproot, they need root networks and associations to acquire necessary nutrients and water for survival (McBride, 1977). The lack of support usually provided by a taproot influences the effect of wind-throw, the main natural cause of redwood mortality, caused by major windstorms that topple the tall trees (Veirs, 1996).

Redwoods also withstand highly saturated soils caused by flooding for limited amounts of time (McBride, 1977; Sawyer, Sillett, Libby, et al., 2000). If existing root networks are flooded, redwoods may temporarily establish new root systems (Barbour et al., 2001). The new aerotropic roots provide oxygen to roots inundated with water (McBride), however redwood trees cannot endure long periods of saturation due to major floods (Barbour et al.).

Redwood is an extremely resilient species, able to grow in areas with very little solar radiation as well as areas with high levels of sunlight (Barbour et al., 2001).

Maximum growth of redwood occurs under full sunlight, although they may establish in heavily shaded areas (McBride, 1977). Growth rates are slower under heavy shade, although if there is a sudden increase in solar radiation, redwoods will respond immediately (Sawyer, Sillett, Libby, et al., 2000). The ability of redwoods to photosynthesize even in dim parts of the forest allows the species to inhabit areas unsuitable for other tree species (Barbour et al.).

Old-growth redwood forests are also unique in composition and structure. These forests contain multiple-layered complex canopies, snags (standing dead trees), downed decaying logs and branches (woody detritus), and shade-tolerant understory species (Sawyer, Sillett, Popenoe, et al., 2000). Snags and complex canopy iterations in old-growth redwood forests offer crucial nesting habitat for endangered bird species (U.S. Fish & Wildlife Service, 1997). They also provide important habitat for nearby aquatic populations, through the recruitment of high volumes of large-diameter wood to streams in close proximity (Benda, Bigelow, & Worsley, 2002). Although old-growth forests are generally the least species rich (Russell & Jones, 2001), this is due to extremely high biomass of *Sequoia sempervirens* (Busing & Fujimori, 2005). Old-growth forests are examples of stable, highly productive communities that experience small-scale or no disturbance over long periods (Huston, 1979).

*Sequoia sempervirens* have several unique properties, differentiating this community from other forest types. Redwood's resilience to fire, insect infestation, disease, water saturation, and variable sunlight are unusually high in comparison to other

tree species. Redwood also has a rare, asexual method of reproduction among conifers. The distinctive characteristics of redwood trees influence community development and forest dynamics.

### *Succession Theory and Coast Redwood Forests*

Several concepts of succession currently exist within the field of forest ecology and forest management. Kimmins (1987) defined succession as the change in communities over time, usually following a disturbance or dramatic change in community composition. Various models of succession attempt to explain the community dynamics involving plant communities (Shugart & West, 1980). Although many models describe vegetation change over time in numerous forest types, currently there is no growth model that accurately represents the unique qualities and characteristics of *Sequoia sempervirens* forest communities. Unusual qualities of redwoods increase the resilience of this species to disturbances that commonly affect other communities. The unique traits of redwood trees are commonly overlooked, resulting in few developmental models that are specifically based on redwood characteristics. However, a brief background of current succession models is necessary in order to understand the differences between the development of non-redwood forests and redwood forests.

The first ecologist to use succession terminology was Clements (1916). Clements' model became widely known as the "Classic" model of succession, which emphasized the development of a community towards a climax, or equilibrium, state (1928, 1936).

Clements defined the climax community as the final and permanent stage of vegetation development within a forest, which provides the primary basis for classification (1936). An integral part of Clements' climax concept is his view on disturbance, which he perceived as having a purely negative effect on community development and prolonged the inevitable movement towards the climax community (Clements, Hanson, & Weaver, 1929). Although influential, Clements' firm view regarding the linear development of plant communities became a point of disagreement among researchers.

Unconvinced of Clements' strict successional model, several other ecologists began to assert differing views on plant development after disturbance. Gleason (1926) surfaced as the founder of a species-specific model. In this model, Gleason attributed plant development to the environmental conditions of the habitat and the migration of neighboring plant communities. According to Gleason, succession was not a fixed mechanism, but depended almost entirely on the behavior of individual plants and the nature of change (1927). Gleason also acknowledged that significant discrepancies existed between seral stages, which may be the result of varying environmental conditions or the scale of the habitat that contained the plant association (1926). Gleason's view was in stark contrast to Clements' previous theory, which led to the emergence of several other models that became increasingly more complex.

Decades later, Watt (1947) developed a new model of succession that operated on a much more local scale. Although Watt still focused on a single-pathway, or linear, model of plant development, his theory differed in application. Watt asserted that

although plant communities changed significantly within seral stages, these changes were proportional at each stage, which led to equilibrium within each sere. He termed this development “phasic equilibrium” to implicate that a steady state existed within each stage of development. Even though the stages within a community were constantly changing, the community itself was in equilibrium with the surrounding environment (Watt). Although Watt altered the view of succession as it related to scale, his premise remained that overall communities were in stable, steady states of development.

Whittaker (1953) was one of the first ecologists to refute the traditional view of succession and include the disturbance regime as a part of the community development process. His “Climax Pattern Hypothesis” model of succession asserted that some level of disturbance is necessary to achieve the climax community, which is not a completely stable state (Whittaker). Whittaker defined a climax community as one that is at balance with localized environmental gradients such as climate, moisture, soil, and surrounding vegetation. Although this model assessed factors other than the dominance of late seral species, a decrease in productivity is still viewed as working against the inevitable linear direction of succession.

Following Whittaker, several theories began to emerge that included multiple pathways for community development. Connell and Slatyer (1977) developed a model that included three pathways for succession and became known as the facilitation, inhibition, and tolerance models of vegetation change. The facilitation theory slightly resembled Gleason's model, since the major method of community development occurs

after the primary successional species altered the environment in a way to make the habitat more suitable for the colonizing species (Connell & Slatyer). Contrastingly, Connell and Slatyer's inhibition model stated that the early recruited species actually inhibited the colonizing species from inhabiting the environment. This theory of vegetation change only allowed for community development to occur once a disturbance removed the primary species from the environment, allowing the colonizing species to take over (Connell & Slatyer). Finally, Connell and Slatyer's tolerance model suggested that change in vegetation did not depend on recruiting or colonizing species, but relied solely on the environmental conditions, which may or may not alter the tolerance of existing species. The multiple pathway models described by Connell and Slatyer expanded the interpretation of successional changes within various communities and allowed for differing forest types to illustrate specific patterns of succession.

Subsequently, a model developed by Cattalino, Noble, Slatyer, and Kessell (1979) also included several pathways that could lead to change in community composition. This model continued from previous multiple pathway models (Connell & Slatyer, 1977) and applied predictive measures to specific individuals and communities. Similar to Whittaker (1953), Cattalino et al. asserted that the disturbance regime within an environment was the main cause for any change of community development, although life histories, adaptive traits, environmental conditions, and the periodicity of disturbance should also be considered. Although successfully applied to canopy species, this particular model failed in its application to understory species, which may have been the



result of untraceable microhabitat features and incomplete historical information (Cattelino et al.).

Tilman (1985) developed a different point of view on community change in his “Resource Ratio Hypothesis” model. Tilman concluded that the specific resources required by individual species were the source of change in plant communities and the impetus for succession. In Tilman's theory, each species within a community was a superior competitor as long as the resources of that species were available. However, once those resources became scarce or obsolete, that species was no longer a strong competitor and composition shifted towards a different species with adequate resources. Tilman focused on each species' necessities for survival, although determining the longevity of these requirements were difficult.

Whitmore (1989) developed a theory on gap dynamics and forest communities, which caused “Gap Phase” succession to gain notoriety. In this contextual theory, Whitmore classified all tree species into two general groups, pioneer species and non-pioneer species, which resulted from gaps in the forest canopy. Whitmore considered the phase of the forest cycle where a gap in the canopy existed as the most important component influencing the floristic composition of the community. Gaps were therefore heterogenous patches, due to the variable structure, diversity, and organization that occurred within the gap (Whitmore). Whitmore's theory was applicable to several forest types, including species that spread through clonal sprouting, such as *Sequoia sempervirens*. However, *Sequoia sempervirens* does not fall discretely into one of the

two categories asserted by Whitmore (pioneer and non-pioneer species). As a tolerant and intolerant species (Sawyer, Sillett, Libby, et al., 2000), redwood can establish itself in large gaps with intensive solar radiation as well as in small gaps with much less sunlight (Barbour et al., 2001). Nonetheless, Whitmore's gap phase model is the most applicable theory to the development of coast redwood communities that experience small-scale disturbances, such as windthrow, which is the most common form of disturbance in unmanaged redwood forests (Hunter & Parker, 1993).

Most of the models of succession described thus far attempted to define community development after some kind of disturbance. However, disturbance in these models did not include human-induced disturbance, such as a timber harvest. Some of the earlier models of succession did not address disturbance at all, while few models attempted to understand succession after a clearcut timber harvest, which resulted in a large canopy gap. One model, developed by Bosch (1971), did attempt to describe forest development after timber harvest, specifically redwood forests. From his model, Bosch concluded that up to 50% of redwoods younger than 800 years old could be harvested without affecting the survival and development of the remaining trees. However, Brussard et al. (1971) found several errors and faulty conclusions in Bosch's model, which led to the dismissal of his recommendations. Evidently, there is considerable disagreement in regard to the development of redwoods after harvest.

Recently, a newer model has been used to predict redwood forest development after harvest through theoretical simulation. This model, the Cooperative Redwood Yield

Output Simulator (CRYPTOS), allows forest managers to calculate timber outputs of actively managed redwood stands (Wensel, Krumland, & Meershaert, 1982). Forest managers also use the CRYPTOS model for other mixed-conifer and Douglas-fir dominated forests, which are very different than redwood dominated forests due to the unique characteristics of *Sequoia sempervirens*. However, the CRYPTOS model was based on theoretical inputs and did not include any empirical data to support the anticipated changes in population. This model is not representative of ecological changes in these forest types and does not take into account other factors within the community (G. Giusti, personal communication, November 8, 2007). More recently, Mahoney and Stuart (2004) developed a mathematical model to predict vegetation distribution in coast redwood forests. Although the model was 75% accurate in application, more empirical data is required for improving baseline information.

Several models of ecological succession attempt to describe and predict vegetation changes over time. However, many models conflict with one another and view succession either as strictly linear (Clements, 1916, 1928, 1936; Watt, 1947) or non-linear (Gleason, 1926, 1927; Whittaker, 1953). A few models were based on a disturbance regime (Cattalino et al., 1979; Connell & Slatyer, 1977; Whitmore, 1989) or other environmental factors (Tilman, 1985). The model developed by Bosch (1971) was extremely controversial and based on a minimal number of localized sample sites. The CRYPTOS model was neither based on empirical data collected in redwood communities, nor did it incorporate unique qualities of *Sequoia sempervirens* (Wensel et

al., 1982). Whitmore's gap phase theory is the closest model that could predict redwood regeneration, although he did not consider human-caused disturbances. This study addresses specific coast redwood characteristics and effects from timber harvest to build a model of succession designed particularly for this species.

### *Diversity Theory*

Diversity is another important concept that is essential in studying biological communities. The most widely accepted approaches to characterizing species diversity incorporate species richness, defined as the number of species within an area, and species evenness, defined as the abundance or distribution of a species in an area (Halpern & Spies, 1995). Community diversity allows for specialized interactions between species and establishment in particular areas, or niches, where each species can thrive (Silvertown, 2004).

Several hypotheses attempt to explain the causes for differences in diversity among communities, including geographical area, historical factors, nutrient availability, environmental stability, environmental stress, disturbance regimes, and biological interactions (Whittaker, Willis, & Field, 2001). However, the results of previous research differ markedly, and there is no consensus on diversity patterns (Huston, 1979). However, Huston developed an innovative approach for diversity analysis. His application of diversity theory involves a comparison of the rates at which populations change approaching a competitive equilibrium (Huston) in addition to traditional

methods. Through comparison of the rates of change, initial patterns of development emerged, which may forecast the diversity conditions within sites of interest.

The primary causes of changes in diversity and habitat heterogeneity in redwood forests following disturbances is not well known. In tropical forests, diversity was relative to scale (Leigh Jr. et al., 2004). On a small scale, neither disturbance nor features of the microhabitat impacted diversity, although on a larger scale, climate and habitat differences explained changes in diversity (Leigh Jr. et al.). Environmental stability, the size of the landscape, and niche opportunities may influence regional differences (Leigh Jr. et al.). Due to the limited distribution of redwood communities, regional scale, landscape complexity, and habitat heterogeneity are necessary components to consider.

### *Restoration Concepts*

A final theoretical context within this field involves restoration. Previous research frequently supports active management of forests as an effective restoration technique (Boe, 1965; Bosch, 1971; Lindquist, 2004a, 2004b; Oliver et al., 1994). This method of restoration involves the reduction of undesirable biomass through thinning regenerating redwood forests. Essentially, removing the surrounding competition increases the productivity and growth of desirable species, such as *Sequoia sempervirens*. However, economically interested parties commonly funded research in support of active removal (Conrad, 1997). This research asserts that the active removal of selected trees increased efficiency by stimulating future growth, which benefits the entire forest (Cole, 1983; Lindquist, 2004b; Oliver et al.). Management that does not include active removal

carries a negative connotation, often referred to as “passive” or “benign neglect” (Carey, 2006).

Although the dominant species may increase in biomass and productivity, current active management policies do not assess the impact to other aspects within the ecosystem. The consequences for wildlife, soil health, water quality, unprofitable species, and understory species are largely ignored. The economic benefit of redwood timber products is the primary focus of these studies (Conrad, 1997). In contrast, studies in different forest communities illustrated that past land use had a significant impact on long-term plant heterogeneity (Fraterrigo, Turner, & Pearson, 2006). A recent study in the redwood forests of Humboldt County, California concluded that several species may recover slowly after timber harvest while some species may not recover at all (Loya & Jules, 2007). Halpern and Spies (1995) also compared plant diversity in unmanaged and managed *Pseudotsuga* (Douglas-fir) forests of the Pacific Northwest and found some species may become extinct locally after intensive management. In addition, Scheller and Mladenoff (2002) compared management practices in the Upper Michigan Peninsula and determined that spatial patterning of understory species were slow to recover in the hardwood forests studied.

The role of fire in the redwood community is another source of controversy in relation to management policies. After European settlement, fire was suppressed within the redwood region to preserve valuable timber, and considered unhealthy for forest development (Fritz, 1930). An historical account of the fire history in the Santa Cruz

Mountains redwood range indicated that fire was a common part of the forest cycle until the nineteenth century (Stephens & Fry, 2005). Stephens and Fry also concluded that the development of redwood forests, both ancient and regenerating, may be dependent on a fire disturbance regime, which is now absent. Recent fire succession models grouped these specialized communities with other mixed conifer forests (Husinga, Laughlin, Fulé, Springer, & McGlone, 2005; Keane et al., 2004), despite differences in composition and character. However, since redwood trees are extremely resilient to fire, due to thick, insulating bark, this forest community is not as susceptible to fire damage as other forest communities (Barbour et al., 2001; Sawyer, Sillett, Libby, et al., 2000).

The comprehensive effects of active management in redwood communities, especially within the central range of California, have not been well studied. Previous research on the regeneration of redwood communities, including fire studies, does not address the specific qualities of redwood forest communities. Empirical evidence is necessary to develop a predictive model for these specialized forests and to determine appropriate restoration methods. This study will provide timely data regarding the development and resilience of redwood communities in order to accurately restore these forests and retain old-growth characteristics.

## Related Research

Patterns of succession in plant communities after a disturbance have been the subject of scientific study for many years. Empirical evidence is necessary to determine the development process indicative of a particular forest community. The results of previous research differ from each other depending on many factors, including the dominant plant species. Due to the unique characteristics of redwoods, this forest community deserves special consideration. Within forest ecology, applicable research regarding succession focused on changes in the dominant tree species in redwood forests, changes in the understory vegetation in non-redwood forests, and changes in the understory vegetation in redwood forests.

### *Succession of Dominant Tree Species in Redwood Forests*

Research in redwood forests exists, but is limited in scope. Most of the empirical research in redwood forest communities focuses on the regeneration of the dominant tree species alone. Research parameters for these studies rarely address community characteristics, such as diversity, or any subsequent effects on the regeneration of understory shrub or herbaceous species.

Fritz (1945) influenced research in redwood communities, establishing an 85-year-old permanent site for data collection and research, later known as the "Wonder Plot" in the Big River Watershed of Mendocino County, California. Over the initial twenty-year monitoring period, overall volume increased dramatically (223,034 board feet), although overall tree density decreased (Fritz, 1945). This one-acre site continues



to provide information on the growth and development of redwood trees by characterizing the high regenerative ability and biomass of this stand. In addition, Fritz (1950) advised forest managers to thin redwood forests in order to increase the volume of residual trees and to maintain redwood as a crop species. Fritz's (1950) studies primarily focused on the economic benefit and profit of the landholder.

Boe (1965) described the natural regeneration of old-growth redwood forests after active management. Experimental cuttings in the Yurok Redwood Experimental Forest attempted to convert old-growth forests to resemble younger, managed second-growth redwood forests to increase timber sales (Boe). The outcome of this study was the increase in timber harvest sales and the reduction of old-growth redwood forests. This research was similar to previous studies in that it was geared towards the economic advantages of harvesting redwood forests.

Powers and Wiant (1970) studied the effects of clearcut logging on old-growth forests in six sites throughout Humboldt and Del Norte Counties. Their study also examined the effect of slash burning after clearcut (Powers & Wiant). Although the burning of slash had no significant effect on the sprouting of residual stumps, excessive logging damage to the remaining stumps did have an effect. A vast majority (92%) of sprouting occurred from the basal area of the tree (Powers & Wiant). Stumps were classified as damaged if at least one-fourth of the original surface of the stump had been removed, covered in soil, or if the stumps were located within three meters of a skid trail (Powers & Wiant). The damaged stumps showed a significant decrease in sprout

production, while on average these stumps produced 50% less sprouts than stumps that were not damaged. Powers and Wiant concluded that excessive damage significantly decreased sprouting due to the crushing of dormant buds in the stump tissue during logging practices.

Bosch (1971) was the first to develop a population model based on the specific regeneration characteristics of *Sequoia sempervirens*. He proposed a mathematical model to predict redwood population growth, which led to his recommendations that timber companies may harvest up to 50% of all redwood trees under 800 years old without affecting the survival and growth of the remaining population (Bosch). However, this model was developed under the faulty assumption that only 8% of redwoods reproduced by sprouting (Bosch); however, current research illustrated that up to 70% of redwoods in a stand may reproduce through clonal sprouting (Duhovnikoff et al., 2004). Several ecologists disagreed and quickly refuted the Bosch model (Brussard et al., 1971), asserting that Bosch used faulty methodology, highly overestimated the survivorship of redwoods once thinned, and inaccurately applied results of one virgin redwood stand to the entire redwood range, regardless of harvest history, location, or environmental factors. The division between redwood forest managers and ecologists began to intensify.

Wensel et al. (1982) developed a predictive model for output, the Cooperative Redwood Yield Output Simulator (CRYPTOS). Forest managers use this computer-simulated prediction model for Douglas-fir (*Pseudotsuga menziesii*), redwood (*Sequoia sempervirens*), and other mixed-conifer forests, although they differ substantially in

individual characteristics and life histories (G. Giusti, personal communication, November 8, 2007). Although this was the first computer-simulated model designed specifically for redwoods, it is questionable in its accuracy, since it is applied to several other forest types. Since the CRYPTOS model was based on theoretical inputs, it lacks empirical data to support the predictions in population change. A few years later, Wensel, Daugherty, and Meerschaert (1986) developed CACTOS, the California Conifer Timber Output, to predict the changes of mixed conifer stands within northern California. This model has similar issues as the CRYPTOS model, since it was also based on theoretical data.

Subsequently, Cole (1983) conducted a study to determine the growth after thinning in a five-acre old-growth redwood stand in Jackson Demonstration State Forest, (Mendocino County, California). Cole randomly selected 15 stumps for thinning and monitoring over a 33-year period. Two years after thinning, stump sprouts exposed to full sunlight grew quickly, stump sprouts in moderate light incurred more competition, growing slower than control plots, and stump sprouts in low light died (Cole). An intermediate group that remained unthinned unexpectedly outgrew all other groups throughout the majority of the study period (Cole). Cole concluded that thinning may not actually increase sprout growth, but may in fact reduce growth.

Oliver et al. (1994), studied three second-growth stands throughout the northern range of redwoods to determine the regenerative nature of the redwood species. They thinned three stands, leaving 25%, 50%, and 75% of original biomass, and left one stand

unthinned for a control comparison. The researchers monitored the stands and recorded basal area and height at the time of thinning and at subsequent five-year intervals for 15 years. Remaining trees responded to the thinning practices by substantially increasing growth production 3.7 times (25% remaining group) and 2.4 times (50% remaining group) compared to control plots (Oliver et al.). In conclusion, Oliver et al. recommended that 50% of the basal area could be removed by thinning without a significant loss in volume of remaining tree species. Productivity and density in the stands chosen for this study were high compared to neighboring stands, although the researchers asserted the conclusions were representative of most second-growth stands in the region (Oliver et al.).

Lindquist (2004a) conducted a 17-year status report and a 29-year status report (Lindquist, 2004b) of precommercially thinned and control plots of *Sequoia sempervirens* within Jackson State Demonstration Forest. In the 17-year report, Lindquist (2004a) chose eighteen 0.4-acre plots and removed various amounts of biomass including 100, 150, 200, 250, or 300 trees. Unthinned plots had the lowest growth in board-feet volume and the smallest diameter on average compared to the other treatments. In the 29-year study, Lindquist (2004b) selected twelve 0.4-acre plots and thinned 25%, 50%, or 75% of the biomass, leaving an unthinned plot for control. Thinning substantially increased the basal area of remaining trees, mainly to replace the removed biomass.

Fujimori (1977) and Busing and Fujimori (2002, 2005) also substantially added to the body of literature in redwood forests by analyzing the composition, structure, volume,

and woody detritus in old-growth stands. Over a 30-year period, Busing and Fujimori determined that *Sequoia sempervirens* retained low rates of mortality, canopy disturbance, and inward growth. There was very little change in species composition, but species exhibited a 'shifting mosaic' within the stand. Redwood increased along edges of gaps and gap size was potentially large (Busing & Fujimori, 2002). In the same forest, stem biomass decreased by 7% and overall biomass declined, but still remained very high and increased in patchiness (Busing & Fujimori, 2005). In conclusion, Busing and Fujimori (2002) stated: "Gaps alone produce enough regeneration to maintain the [redwood] species."

Studies on the regeneration of redwood trees differ substantially with respect to their findings and conclusions. Fritz (1945, 1950), Lindquist (2004a, 2004b) and Oliver et al. (1994) asserted that active restoration, or thinning, may benefit the community by increasing the volume of biomass production, which supported continuing harvesting in second-growth stands. Some studies focus solely on economic benefits (Boe, 1965) or did not use empirical data to support conclusions (Wensel et al., 1982). However, Powers and Wiant (1970) and Cole (1983) found that thinning decreased the ability of coast redwood to sprout due to logging damage or environmental conditions. In addition, Brussard et al. (1971) refuted Bosch's (1971) population model, which supported active removal of biomass. Furthermore, Busing and Fujimori (2002, 2005) determined that small-scale disturbances and natural processes of community development in old-growth forests were sufficient management approaches. Nonetheless, none of these studies

addressed overall community diversity or changes in understory communities in redwood forests following a disturbance.

#### *Succession of Understory Vegetation in Non-Redwood Forests*

Research that analyzed understory composition, species interaction, and diversity in forests largely remains limited to other forest communities. The parameters and findings of these studies may be applicable to other forest types, although they do not take into account the unique characteristics of redwoods. Several forest types have been studied to determine the effects on shrub and herbaceous cover following clearcut harvest. Although a number of studies exist in several forest communities, they vary dramatically in their results and do not offer any consensus.

Globally, the effect of logging on the regenerative nature of vegetation communities has been explored for many decades. In a Canadian black spruce forest, Brumelis and Carleton (1989) compared logged and unlogged wetland forests and found the major influence on plant recovery after logging was the type and availability of nutrients in the soil. After logging, tree species recruited to each stand very slowly, however understory perennial rhizome plants did recover and sprout (Brumelis & Carleton). In a tropical Amazonian forest, logging intensity did not affect herbaceous species richness or composition on the eight plots sampled, five of which were controls (Costa & Magnusson, 2002). Skid tracks, however, did have an impact on future plant development, favoring invasive colonizers (Costa & Magnusson). Dignan and Bren (2003) evaluated the effects of solar radiation on understory species after logging

occurred near riparian zones of a forest in southeast Australia. Harvest practices created a sharp contrasting edge between logged and unlogged areas, with an edge influence of up to 100 meters in the unlogged portions.

The majority of research analyzing the effects of logging on succession occurred in the eastern portion of the United States, primarily in the Appalachian range. Duffy and Meier (1992) compared nine old-growth hardwood stands to nine second-growth hardwood stands. Neither herbaceous cover nor richness changed with time in the second-growth forests, suggesting that herb species did not recover on the current harvest rotation of 40-150 years (Duffy & Meier). Gilliam, Turrill, and Adams (1995) compared diversity of overstory and understory species between two 20-year old previously clearcut stands and two 70-year old previously selectively-cut stands in an Appalachian hardwood forest. They concluded competition pressure caused tree species evenness to decrease over time, but found no significant change in diversity. This result may be due to the fact that the study compared two very different harvest methods. In a subsequent study, Gilliam (2002) also found no significant difference in herbaceous cover or diversity in a young forest versus a mature forest after clearcut harvest. Gilliam did see a significant change in young stands, which had 2.5 times the tree density of mature stands, while mature stands had almost twice the basal area as young stands (2002). However, the stands compared in this study did not have the same past land use histories, which may have affected the results.

Previous studies in the eastern United States by Gilliam and Turrill (1993) and Gilliam et al. (1995) explored past land use and environmental factors in vegetation succession. These studies determined that allogenic factors, such as soil quality, initially influenced community development, while autogenic factors, such as canopy development, became more important in influencing plant succession as the stand aged (Gilliam & Turrill; Gilliam et al.). Yorks, Dabydeen, and Smallidge (2000) determined that environmental factors including soil moisture and age of stand primarily influenced the distribution of species. Recently, Fraterrigo et al. (2006) found that nutrient availability determined vegetation development in manipulated and unmanipulated forests and past land use had long-lasting effects on the heterogeneity of plant species. In a northern lower Michigan *Populus* forest that was previously clearcut, Roberts and Gilliam (1995) compared young second-growth forests and mature second-growth forests. They found no significant difference in diversity, species composition, or soil structure between the 52 sites sampled.

Little research exists in the western region of the United States that specifically determined the effect on plant regeneration after clearcut timber harvest. Dyrness (1973) recorded plant composition over seven years in a *Pseudotsuga menziesii* var. *menziesii* dominated old-growth forest in western Oregon following logging and burning. The post-logged unburned sites retained a variety of residual species, but also became habitat for several invader species (Dyrness). Scheller and Mladenoff (2002) studied species composition, diversity, and spatial patterns in 12 stands of different harvest history,



including old-growth, clearcut, and selective cut. They found negligible differences between herbaceous understory species between all stands, but noticed an increase in heterogeneity and patchiness in old-growth stands (Scheller & Mladenoff).

Studies regarding vegetation change over time in non-redwood dominated communities were comprehensive but differ substantially in their findings. Previous logging had no effect on herbaceous richness, diversity, and composition in several studies (Costa & Magnusson, 2002; Duffy & Meier, 1992; Gilliam, 2002; Gilliam et al., 1995; Roberts & Gilliam, 1995; Scheller & Mladenoff, 2002). This could have been due to a minimal number of sample sites, which may not have accurately represented the actual changes in vegetation composition. The lack of significance also suggests that plant species were not able to recover on the current harvest rotations. However, Dyrness (1973) found a large increase in understory coverage since harvest. In addition, Dyrness, along with Costa and Magnusson, observed a large increase in invasive species after logging in young stands. The evidence from previous research implies patterns of succession are still unclear in other forest types.

#### *Succession of Understory Vegetation in Redwood Forests*

Few studies address logging effects specifically on the understory species in redwood forests. The studies that do address several components of community development, and not simply the growth of *Sequoia sempervirens* itself, were limited to specific regions of the redwood range. In addition, these previous studies do not have sufficient sample data to extrapolate results to other regions.

The study of the floristic distribution within redwood forests began when Waring and Major (1964) surveyed and characterized the vegetation in 30 coastal redwood forests in Humboldt County, California. They applied a gradient analysis to determine the most important environmental factors that influenced community development: moisture, nutrients, light, and temperature (Waring & Major). Redwoods primarily thrived within moderate climates in moist, fertile soils containing high levels of nitrogen (Waring & Major).

Significant research regarding the regeneration of understory communities in northern redwood forests began several years ago. Rivas-Ederer and Kjeldsen (1998) evaluated community dynamics and species changes over time in Jackson State Demonstration Forest. No significant findings came out of this study. This could be attributed to several factors, including an inadequate number of study sites, the application of herbicides to remove undesirable species after harvest, or the replanting of species following clearcut. In this study, the post-harvest management was not indicative of natural regeneration. Jules (1998) conducted a survey on the effects of clearcutting on *Trillium ovatum*, a common coast redwood herbaceous perennial. Jules found that clearcutting, along with the replanting that followed, destroyed nearly all trillium, with an increased mortality at forest edges. Trillium did not recover from logging practices, although harvest occurred over thirty years prior, and became limited to old-growth forests (Jules). In addition, along forest edges trillium plant populations experienced a decrease in seed production and an increase in seed predation (Jules & Rathcke, 1999).

Recently, Loya and Jules (2007) evaluated the impacts to understory species as well as the dominant tree species in the redwood forests of Humboldt County. They concluded environmental conditions, seral phase, and landscape affected sampling efficacy (Loya & Jules). The authors also illustrated that herb cover, non-native herb cover, and species richness decreased over time and concluded that some plant species may take longer to recover if managed in a regenerating second-growth redwood forest (Loya & Jules). A few old-growth indicator species did not exist in any second-growth sites, although old-growth forests were not statistically different in species richness than younger plots (Loya & Jules). This study examined new aspects of the redwood forest, although more data comparing consistent land ownerships and past land uses is necessary.

Russell and Jones (2001) studied the effects of logging on adjacent old-growth stands in order to determine the relative effects of clearcut harvest on preserved areas. Their results indicated that there is an effect on adjacent old-growth forests as far as 200 meters inward (Russell & Jones). The observable edge effect effectively reduced the size of the core habitat and old-growth characteristics. They also observed an initial increase in hardwood tree density immediately following harvest due to the rapid growth of colonizing species, which thrived in the temporarily exposed and sunlit areas (Russell & Jones). Over time the dominance of these species decreased, due to the increased domination and growth of *Sequoia sempervirens* (Russell & Jones).

The tendency of studies in redwood communities is to direct objectives solely toward specific tree species while ignoring the impact on understory species or community diversity. Most studies that addressed impacts on understory communities do not take into account the distinctiveness of *Sequoia sempervirens*. Research that does consider redwood characteristics and community structure did not address the effect of logging on the harvested area itself (Russell & Jones, 2001) or lacked an adequate number of sample sites (Rivas-Ederer & Kjeldsen, 1998; Loya & Jules, 2007). This study addresses changes in regenerative patterns and diversity of all floristic levels of the redwood forest community following clearcut timber harvest.

## Research Objectives

The objectives of this study were to assess vegetation community development of naturally-regenerating coast redwood stands at various ages since timber harvest and to provide information for restoration efforts. Null hypotheses addressed include the following:

1. Stand parameters, including tree density, frequency, dominance, canopy cover, and tree species diversity will not change significantly over time following timber harvest or compared to old-growth communities.
2. There will be no significant change in the dominance or importance of specific tree species following timber harvest or compared to old-growth communities.
3. Understory parameters, including herbaceous and shrub cover, total understory cover, and understory species diversity, will not change significantly following timber harvest or compared to old-growth communities.
4. There will be no significant change in the cover of specific understory species following timber harvest or compared to old-growth communities.

## Methods

### *Study Area*

The study area for this project was the Big River Watershed and surrounding areas in Mendocino County, California, consisting of more than 2,968 hectares (approximately 7,334 acres) of regenerating coast redwood forest (California Department of Parks & Recreation, 2006). The Big River Unit, a recently purchased portion of the Big River Watershed, is located in the central region of the redwood forest range and interfaces with the ocean at the Big River Estuary in Mendocino. The vegetation is characteristic of central redwood forests and includes various species adapted to the canopy, sub-canopy, and understory layers of the area. Various ages of regenerating second-growth forests exist within this watershed, providing the basis for site selection.

The Big River supports several sensitive plant species, animal species, and vegetation communities (California Department of Parks & Recreation, 2006). A variety of species add to the diversity of the alluvial terraces of the Big River Watershed, such as the redwood/redwood oxalis association (Smith & Wheeler, 1992). The soils of the area are derived from the Franciscan assemblage, which mainly consist of sandstone and marine sediments. Soils are variable, but may be ultramafic (high in magnesium and iron) or consist of loamy clay, which redwood does not invade (Zinke, 1988). Redwood trees thrive in young, fertile soils with abundant nutrients and moderate pH levels (Zinke). Erosion, sediment deposit, and runoff largely affect the available nutrients and soil composition.

The climate of the central redwood region within Mendocino County and the Big River Watershed varies substantially from coastal to inland areas. Typically, summers are warm and sunny, with intermittent fog along the coast. Inland fog is less common and usually dissipates by mid-morning. The characteristic fog of coastal California is crucial for redwood development and may input up to 30% of water each year (Burgess & Dawson, 2004). Winters are cool and wet with an annual precipitation of approximately 2,500 mm or more (Sawyer, Sillett, Popenoe, et al., 2000).

The Big River was an ideal location for this study due to the presence of several even-aged regenerating redwood stands that received no post-harvest manipulation. Unmanaged forest stands were necessary for this study to determine qualities that are indicative of natural regeneration processes. In addition, the large size of the Big River Watershed allowed for sampling of contiguous forest stands within sites while avoiding neighboring edge effects from adjacent disturbances (Russell & Jones, 2001).

### *Study Design*

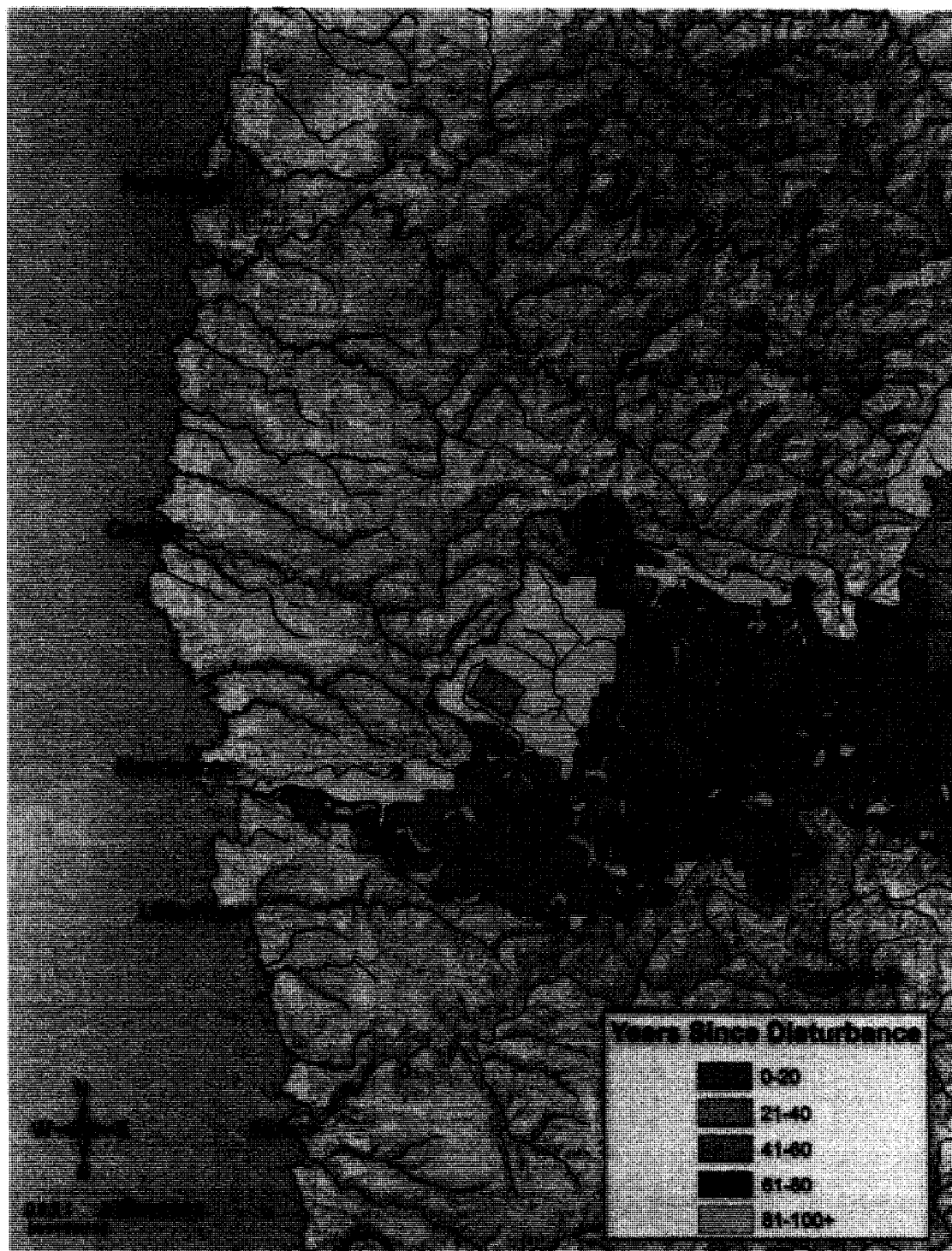
Site selection for this project depended heavily on the availability of detailed logging history maps, with representative patches of community age since timber harvest. A watershed assessment report, compiled by Rob Rutland (2002), Forest Practice System Manager for the Santa Rosa California Department of Forestry and Fire Protection, provided detailed land use information. Rutland's report, *Big River Land Use History: 1852-2001*, listed each activity (clearcut, seed-tree removal, shelterwood cut, etc.), completion year, decade mid-point for each activity, and level of disturbance for each

activity (high, moderate, or low) for the entire Big River Watershed. Data sources used to compile this report included the California Department of Forestry and Fire Protection, North Coast Watershed Assessment Program, Forest Practice GIS (Santa Rosa), Graham Matthews and Associates, and Jackson Demonstration State Forest. In addition to State Timber Harvest Plans, Rutland compiled data using personal communications and aerial photos to determine historical coverage in the Big River watershed. Rutland's methods using aerial photographs for identifying past vegetative cover are consistent with previous research (Costa & Magnusson, 2002; Dignan & Bren, 2003).

Data from Rutland's (2002) report provided the necessary foundation for selecting sites based on the criteria for this study. Rutland's data and U.S. Geological Survey 10-meter resolution Digital Elevation Model base layers were compiled using ArcMap© 9.2 to produce a timber harvest map (Figure 1) and a site map of regenerating stands (Figure 2) within the Big River Watershed. Site criteria included:

- Even-aged stands;
- Dominated by *Sequoia sempervirens*;
- Previously clearcut harvested;
- Located within the Big River Watershed;
- No post-harvest management such as seeding, thinning, planting, etc.;
- Currently unmanaged and relatively undisturbed stands;
- Large enough for adequate sampling without edge effects;
- Feasibly accessible.





*Figure 1.* Timber harvest history, Big River Watershed, Mendocino County.

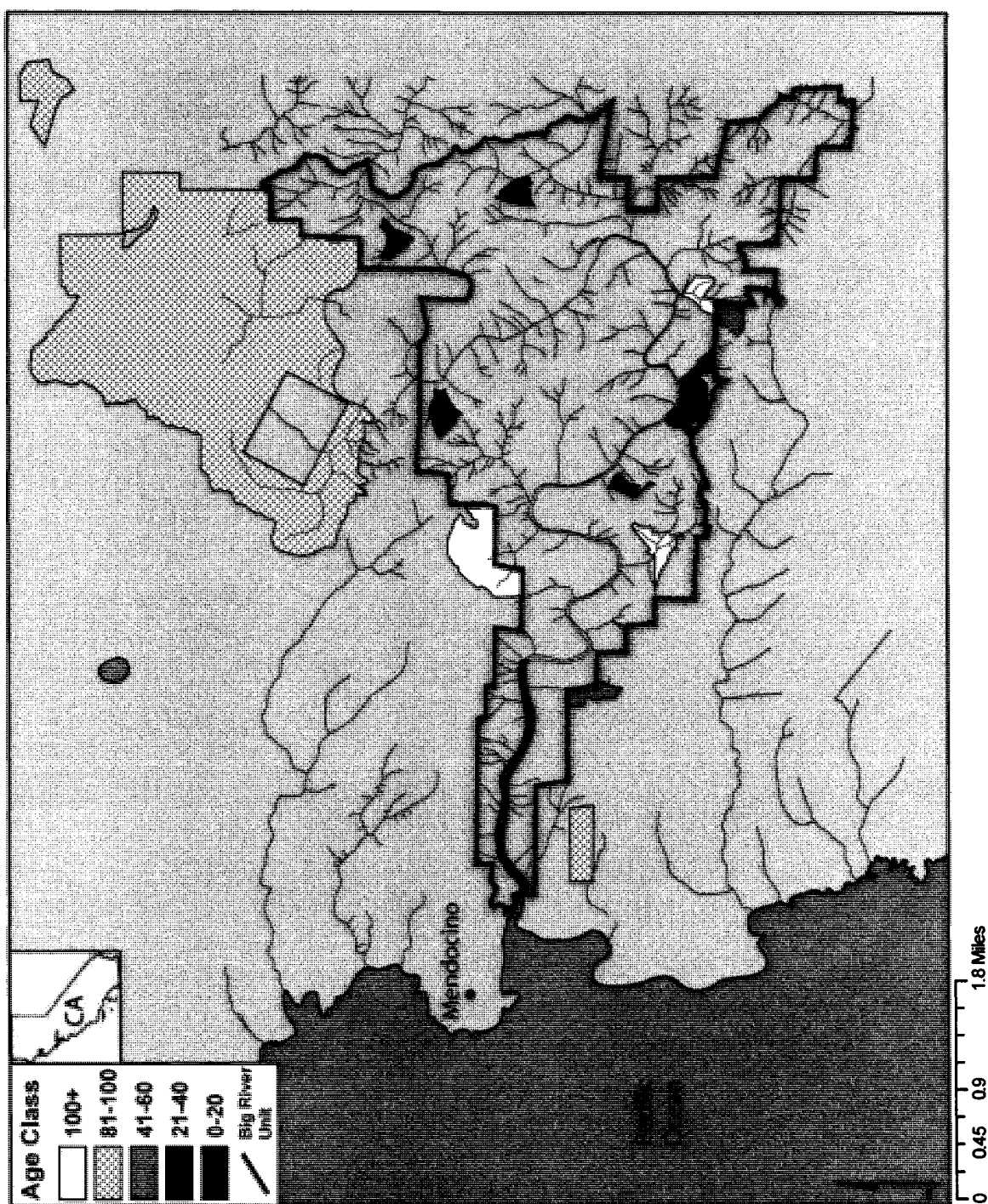


Figure 2. Regenerating sample sites, Big River Watershed, Mendocino County.

Non-response variables, including slope and aspect, were randomized (Appendix A).

Younger sites generally had steeper slopes due to recent advancements in logging methods. Within sites, several criteria were also implemented:

- 20 meters from adjacent plots;
- 10 meters from special habitats, such as riparian areas and rock outcroppings;
- 200 meters from adjacent age class boundaries (if age difference between sites was greater than 20 years) and main access roads;
- Not located on developed logging roads or trails.

Three sites were selected in each age class, for a total of 18 sites. Most age classes were located within the Big River Unit, however additional sites were established in surrounding areas to include a broad spectrum of age since harvest. These areas included the Russell redwood property, southwest of the Big River Unit, and Jackson State Demonstration Forest, northeast of the Big River Unit. Both of these sites had sufficient logging data available and met the criteria for site selection. No sites existed within the 61-80 year range of regenerating forest that fit the criteria for this study.

Unlogged old-growth stands were sampled as control sites and compared to regenerating stands. These sites were displayed using ArcMap© (Figure 3) and included the Russell redwood property, Montgomery Woods State Reserve (located east of Mendocino along the Comptche-Ukiah Road), and Hendy Woods State Park (southwest of the Big River Watershed off Highway 128). All of the old-growth sites contained preserved ancient redwood groves with little obvious human impact.

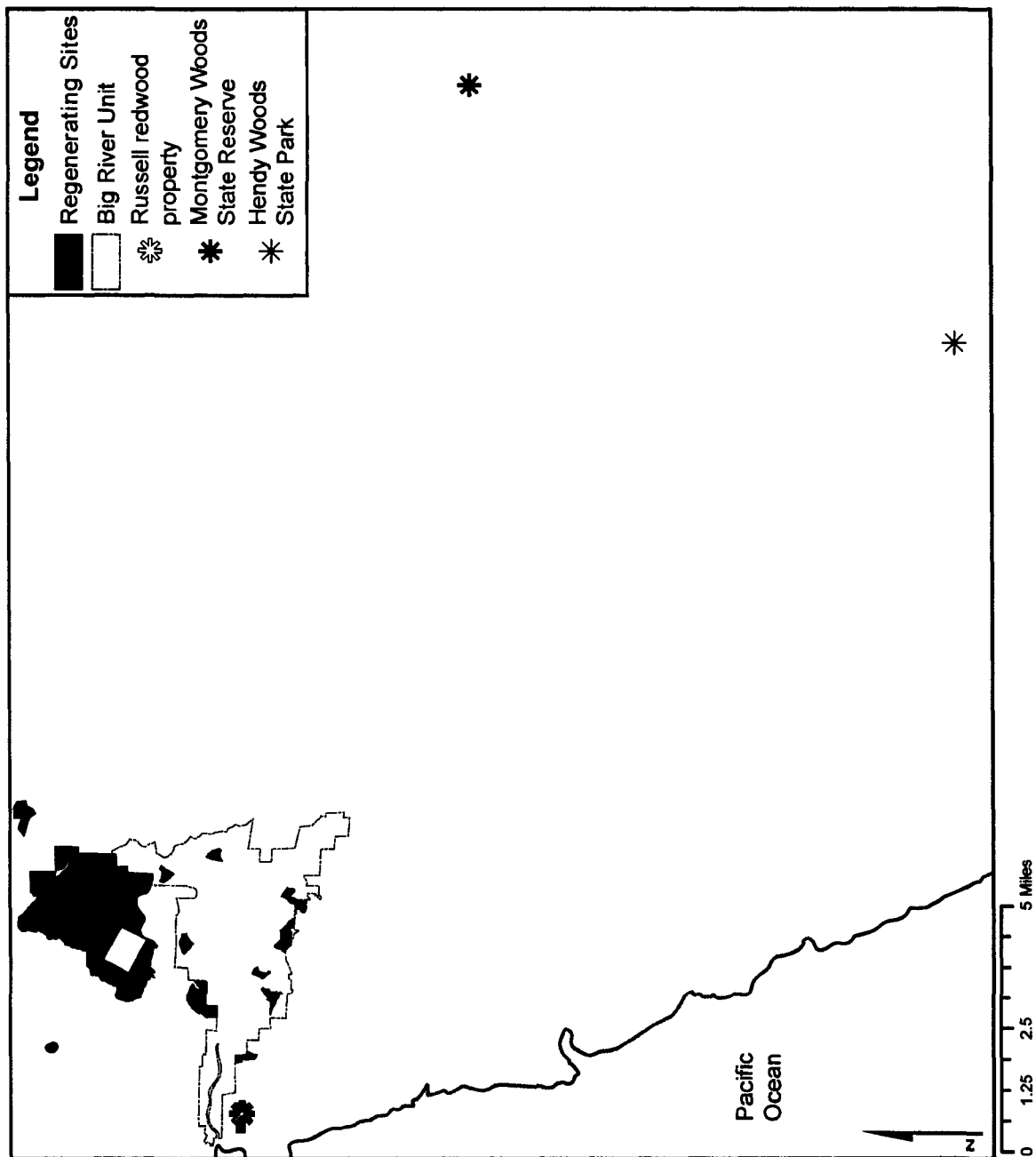


Figure 3. Regenerating stands and old-growth stands, Mendocino County.

The Species-Area Curve (Cain, 1938) was used to determine the number of plots necessary for sampling, consistent with previous vegetative research (Loya & Jules, 2007; Russell & Jones, 2001). A pilot study conducted in late spring of 2007 indicated that 20 plots was the minimal number necessary in each age class for a representative sample size. Using ArcMap© 9.2 software with the AlaskaPak© Extension, 20 circular plots within each site were randomly selected. Six age groups, with three sites in each, resulted in a total of 360 plots for this study.

A handheld Garmin© GPS receiver located randomized sample plots. When sites were unsuitable for sampling, plots were relocated a minimum of 100 meters away in a random direction by spinning a compass. Once at a suitable plot, field tape was used to measure 20 meter-diameter plots (0.031 hectares). The plot size used for this study is consistent with previous research (Russell & Jones, 2001) and utilizes the maximum feasible size, proposed by Kenkel and Podani (1991) for sufficient sampling. At the center of each plot, slope and aspect were assessed using a Brunton GeoTransit© compass. Longitude and latitude were recorded using a handheld Garmin© GPS receiver and canopy cover was measured using a Forestry Suppliers© Spherical Crown Densiometer. Within each plot, every tree species, including seedlings and saplings, was identified and recorded. The diameter at breast height of each tree species taller than one meter was measured using a 10-meter Forestry Suppliers© Metric Diameter Tape. Trees less than one meter in height were classified as seedlings. Utilizing plant identification keys (Becking, 1982; Lyons & Cuneo-Lazaneo, 2003; Smith & Wheeler, 1992; Watts,

2002) and following the Jepson Manual (Hickman, 1993) every understory species was identified and recorded. Visual estimates were used to evaluate the percent coverage of herbaceous and plant species (Dyrness, 1973; Gilliam et al., 1995; Gilliam & Turrill, 1993; Scheller & Mladenoff, 2002), equivalent to percentage diagrams for estimation described in Compton (1985).

### *Analytical Methods*

Stands were analyzed using a chronosequence analysis across various age classes after timber harvest. Variation between sites, including slope, aspect, soil, harvest procedures after sites were decommissioned, and management history, was minimized to the extent feasible. However, variation may limit the level of strict comparative analysis between sites and affect the outcome of this study to a certain degree.

Data were first entered into an Excel© spreadsheet. Appropriate variables were then selected for analysis using Aabel© 2.4 statistical software. Descriptive statistics provided a preliminary analysis of the data collected (Duffy & Meier, 1992). Before statistical analysis, tree dominance, tree density, tree frequency, tree importance, tree diversity, understory diversity, and understory cover were calculated.

For tree species, the diameter at breast height measurement was used to calculate basal area ( $m^2$ ). From this calculation, total dominance and single species dominance for each tree species in every plot was calculated. Total tree dominance (the sum of all basal areas per hectare) and individual species dominance (individual species basal area per hectare) were calculated for all species. Total tree density (total trees in each plot per

hectare) was calculated and reported for each plot. Tree frequency (the total number of plots in which a tree species occurs per total plots sampled) was calculated for all canopy species found in each plot.

Importance Value was calculated by combining relative dominance, relative density, and relative frequency of each tree species, consistent with previous research (Curtis & McIntosh, 1951; Holl, 2002; Jenkins & Parker, 2001; Skeen, 1973). Relative dominance was defined as the basal area of a single tree species in a plot per total basal area of all tree species in a plot. Relative tree density was defined as the number of a single tree species in each plot per total number of tree species in each plot. Relative frequency was defined as the frequency of a single species in each plot per total frequency of all tree species found in each plot. The summation of these three values, the Importance Value, was calculated for each tree species.

Diversity of tree species and understory species was compared within and between sample plots using species richness, species evenness, and the Shannon-Weiner Diversity Index. In the Shannon-Weiner Diversity Index (DeJong, 1975; Gilliam, 2002; Russell & Jones, 2001),  $p$  is the proportion of species  $i$  in the total sample ( $p_i$ ), which is then multiplied by natural log ( $\ln p_i$ ). The result is summed across all species and multiplied by -1 for the final index value. By dividing the Shannon-Weiner Diversity Index value by the natural log of species richness (the total number of species), evenness was also calculated. These indicators of diversity aided to further explain overall species diversity.

Understory species cover was determined by visually estimating the area covered by a single species in reference to the area of the entire plot. Understory cover was then calculated by multiplying the area covered by each species by the number of square meters in a hectare. Only native species occurring in at least 10% of the plots sampled (minimum of 36 plots) were reported. Exotic species did not occur in at least 10% of the plots sampled, but were reported for biological significance.

For initial statistical analysis, a Principal Components Analysis (Karadzic & Popovic, 1994; McCarthy, Hammer, Kauffman, & Cantino, 1987) characterized differences in sites according to age class. Before analysis, each variable was tested for skewness. Every response variable was input into the Principal Components Analysis, including species that occurred in more than 10% of the plots sampled (Appendix B). Factors explaining at least 15% of the variation in the data were reported, including significant component loadings greater than absolute 0.300.

One-Way ANOVA analyses (DeClerck, Barbour, & Sawyer, 2005; Fraterrigo et al., 2006; Lindquist, 2004a) were used to illustrate significant differences between regenerating redwood stands and unharvested old-growth stands. Data were tested for normality using a skewness test and an Aabel© Probability Chart, which displayed the cumulative distribution of the data relative to a normal distribution function (Gigawiz, 2007) to graphically illustrate any deviation from skewness. Total tree dominance, *Lithocarpus densiflorus* dominance, *Pseudotsuga menziesii* var. *menziesii* dominance, *Tsuga heterophylla* dominance, *Abies grandis* importance, *Umbellularia californica*



importance, *Tsuga heterophylla* importance, summed herb cover, exotic species cover, *Oxalis oregana* cover, *Viola sempervirens* cover, *Tiarella trifoliata* var. *unifoliata* cover, *Rhododendron macrophyllum* cover, *Gaultheria shallon* cover, and *Toxicodendron diversilobum* cover were positively skewed and transformed using a natural log ( $\log_e$ ) transformation. Data were tested for homogeneity using the Bartlett's *Chi-Square* statistic. Data did not violate the homogeneity assumption. Additional post hoc comparisons within the ANOVA were performed using the Bonferroni Test for differences between means.

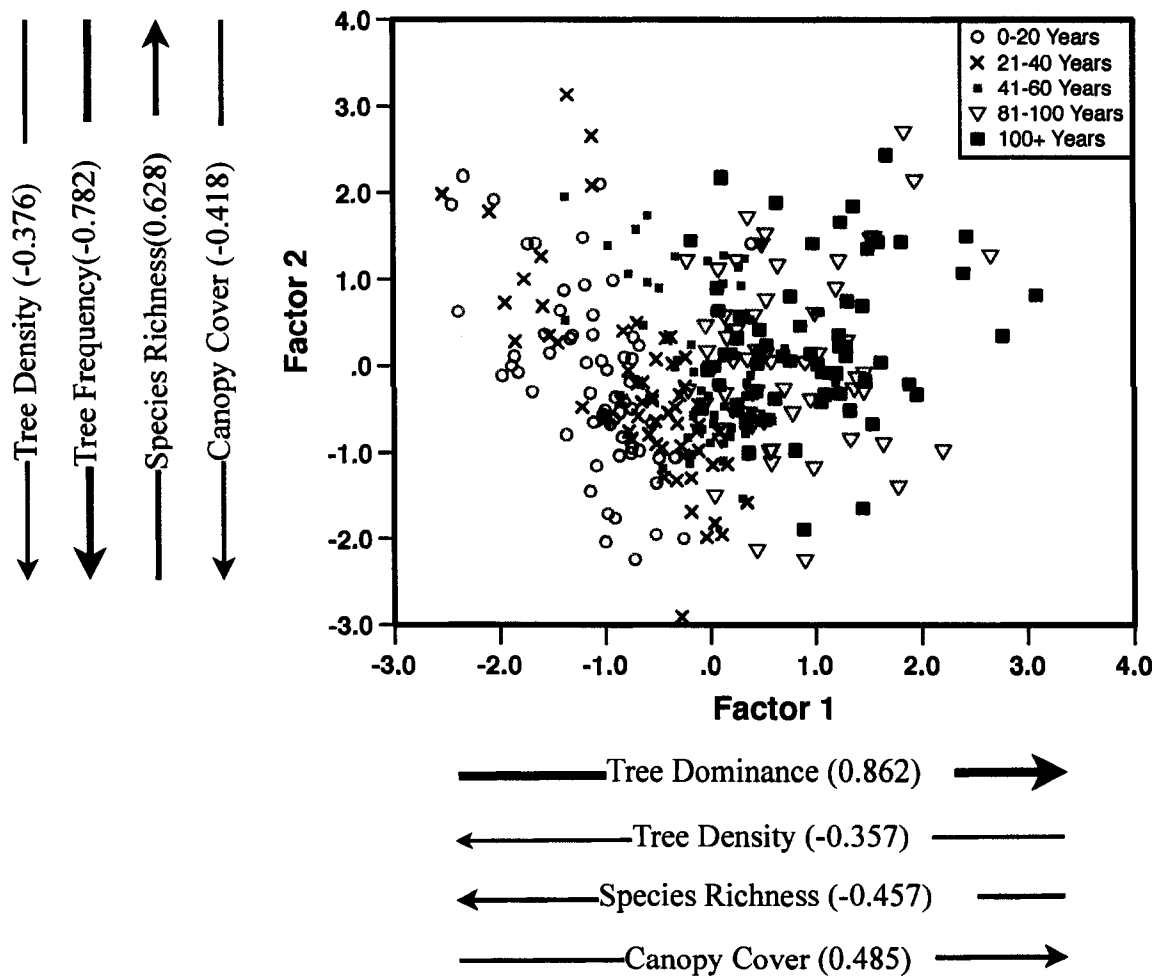
Linear regression (DeClerck et al., 2005; Lindquist, 2004a, 2004b; Koch, Sillett, Jennings, & Davis, 2004) was used to illustrate significant changes and trends in regenerating stands over time following clearcut timber harvest not demonstrated in the One-Way ANOVA results. Regression analysis for total tree density and total basal area were included in the analysis. Linear regression was also used to illustrate the change in exotic species over time after clearcut harvest. Although still significant, r-squared values for these models were very low due to the lack of exotic species in older stands. The significance level for a priori analyses was set at  $\alpha = 0.05$ . Post hoc analyses using the Bonferroni Test for Differences Between Means used an adjusted significance, which was calculated by dividing the original significance level (0.05) by the number of groups compared (15), resulting in an adjusted level of  $\alpha = 0.003$ .

## Results

The results from the statistical analysis illustrated several significant trends over time in regenerating coast redwood communities of the Big River Watershed. Using Aabel© 2.4 Gigawiz software, the One-Way ANOVA and linear regression analyses yielded significant results. All species reported occurred in at least 10% of the total plots sampled (Appendix B).

### *Overall Relationships*

There was a significant relationship between several response variables and time following clearcut timber harvest. Initial evaluation involved a Principal Components Analysis (Figure 4). Factor 1 explained 26.14% of the variance in the data. Factor 2 explained 17.76% of the variance. Total tree density, or number of trees per hectare, was significantly correlated with Factor 1 scores (-0.357), as were total tree dominance, or basal area (m<sup>2</sup>) per hectare (0.862), and percent canopy cover (0.485). Species richness, or total number of different species (0.628), correlated with Factor 2 scores. Canopy cover (-0.418), tree frequency, or total number of plots tree species occurred per total plots sampled (-0.782), and tree density, or total number of trees per hectare (-0.376), negatively correlated with Factor 2 scores. Younger stands (0-40 years old) distinctly separated from older stands (81-100+) along Factor 1. Young stands were associated with high densities of tree species and low levels of tree species dominance. Older stands were characterized as having low tree densities and high levels of tree dominance.



*Figure 4.* Principal components analysis with component loadings characterizing regenerating redwood stands of the Big River Watershed.

### *Stand Parameters*

Several stand parameters changed significantly following clearcut harvest. A One-Way ANOVA comparing total tree density and age showed young stands differed significantly from older stands ( $F(5, 360)=27.599, p<0.001$ ) (Figure 5). Post hoc analysis using the Bonferroni test also yielded significant results (Table 1). A significant negative linear regression ( $y = -9.049x + 1966.75$ ) between total tree density and time since harvest supported these results ( $p<0.001, r^2=0.151$ ). A significant One-Way ANOVA compared canopy cover and age ( $F(5, 360)=8.470, p<0.001$ ) (Figure 6). Post hoc analysis illustrated mean canopy cover significantly differed between age classes (Table 2).

Diversity of tree species changed significantly with stand age. A One-Way ANOVA between mean tree species richness in regenerating forests and old-growth forests ( $F(5, 360)=17.121, p<0.001$ ) showed a significant change with time from harvest (Figure 7). Additional analysis also illustrated there were significant differences between mean tree species richness between age classes (Table 3). A One-Way ANOVA between tree species diversity and age class indicated a significant difference ( $F(5, 360)=9.100, p<0.001$ ) (Figure 8). Additional post hoc analysis also yielded a significant difference between mean diversity values and age class (Table 4). Overall species richness (the total number of different species per sampled area) showed a significant relationship with age since harvest ( $F(5, 360)=7.278, p<0.001$ ) (Figure 9). Post hoc analysis illustrated significant differences between mean total species richness and age classes (Table 5).

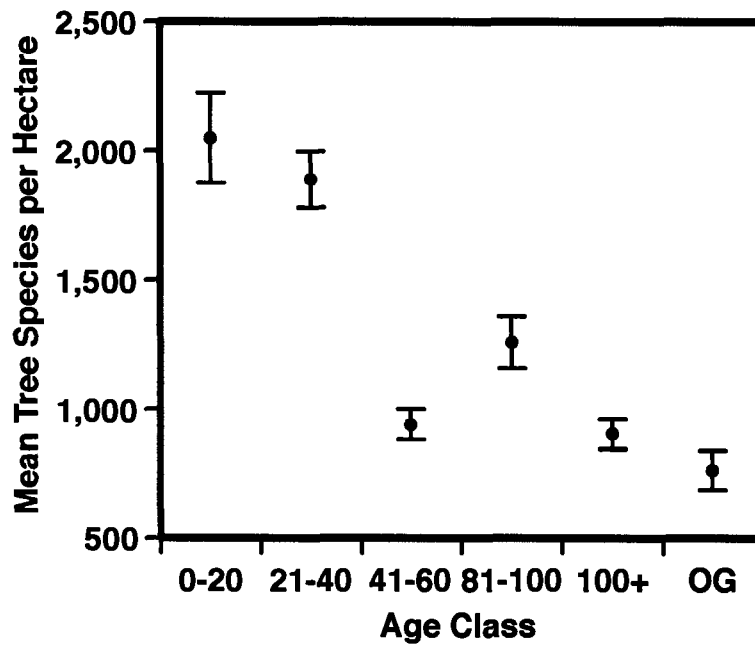


Figure 5. One-Way ANOVA between mean tree density and age class in regenerating and old-growth forests.

Table 1. Mean tree species density post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	159.677	0.780	0.437	No
0-20 - 41-60	1108.065	6.049	< 0.001	Yes
0-20 - 81-100	788.710	3.941	< 0.001	Yes
0-20 - 100+	1141.935	6.253	< 0.001	Yes
0-20 - OG	1284.946	6.737	< 0.001	Yes
21-40 - 41-60	948.387	7.733	< 0.001	Yes
21-40 - 81-100	629.032	4.285	< 0.001	Yes
21-40 - 100+	982.258	8.065	< 0.001	Yes
21-40 - OG	1125.269	8.420	< 0.001	Yes
41-60 - 81-100	-319.355	2.781	0.006	No
41-60 - 100+	33.871	0.421	> 0.5	No
41-60 - OG	176.882	1.814	0.072	No
81-100 - 100+	353.226	3.100	0.002	Yes
81-100 - OG	496.237	3.922	< 0.001	Yes
100+ - OG	143.011	1.483	0.141	No

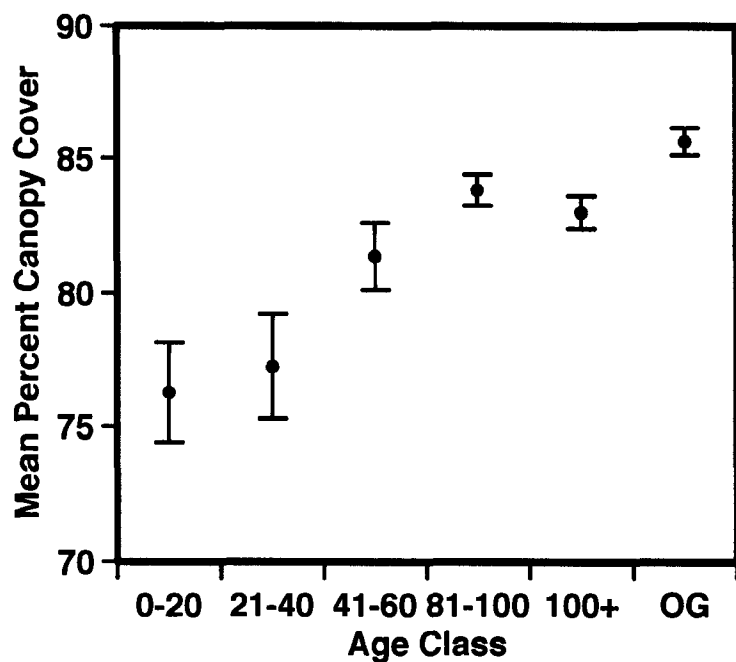


Figure 6. One-Way ANOVA between mean canopy cover and age class in regenerating and old-growth forests.

Table 2. Mean canopy cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-0.983	0.361	> 0.5	No
0-20 - 41-60	-5.100	2.281	0.024	No
0-20 - 81-100	-7.550	3.867	< 0.001	Yes
0-20 - 100+	-6.733	3.432	< 0.001	Yes
0-20 - OG	-9.383	4.844	< 0.001	Yes
21-40 - 41-60	-4.117	1.764	0.080	No
21-40 - 81-100	-6.567	3.181	0.002	Yes
21-40 - 100+	-5.750	2.774	0.006	No
21-40 - OG	-8.400	4.099	< 0.001	Yes
41-60 - 81-100	-2.450	1.803	0.074	No
41-60 - 100+	-1.633	1.190	0.236	No
41-60 - OG	-4.283	3.205	0.002	Yes
81-100 - 100+	0.817	0.978	0.330	No
81-100 - OG	-1.833	2.369	0.019	No
100+ - OG	-2.650	3.321	0.001	Yes

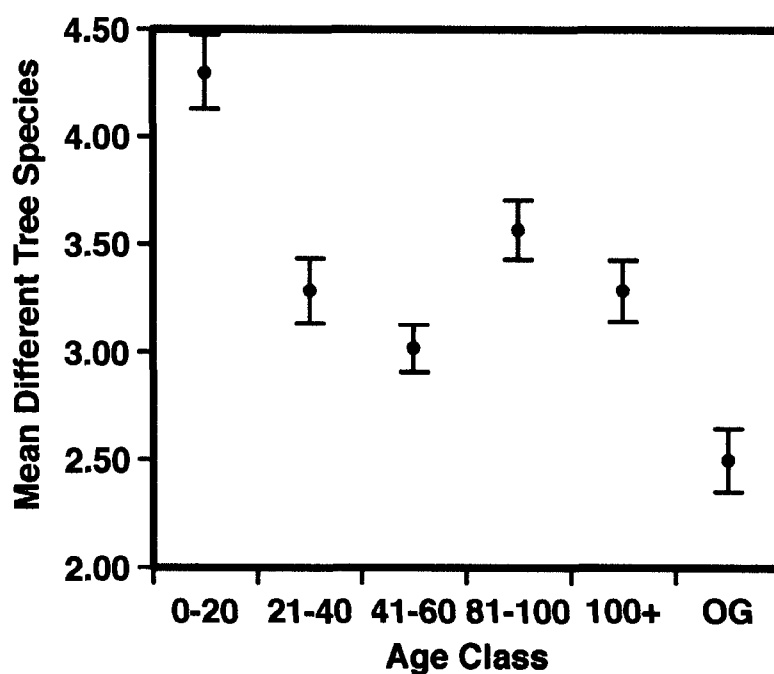


Figure 7. One-Way ANOVA between mean tree species richness and age class in regenerating and old-growth forests.

Table 3. Mean tree species richness post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	1.017	4.426	< 0.001	Yes
0-20 - 41-60	1.283	6.202	< 0.001	Yes
0-20 - 81-100	0.733	3.276	0.001	Yes
0-20 - 100+	1.017	4.524	< 0.001	Yes
0-20 - OG	1.800	7.904	< 0.001	Yes
21-40 - 41-60	0.267	1.441	0.152	No
21-40 - 81-100	-0.283	1.391	0.167	No
21-40 - 100+	0.000	0.000	> 0.5	No
21-40 - OG	0.783	3.766	< 0.001	Yes
41-60 - 81-100	-0.550	3.096	0.002	Yes
41-60 - 100+	-0.267	1.491	0.139	No
41-60 - OG	0.517	2.830	0.005	No
81-100 - 100+	0.283	1.430	0.155	No
81-100 - OG	1.067	5.294	< 0.001	Yes
100+ - OG	0.783	3.868	< 0.001	Yes

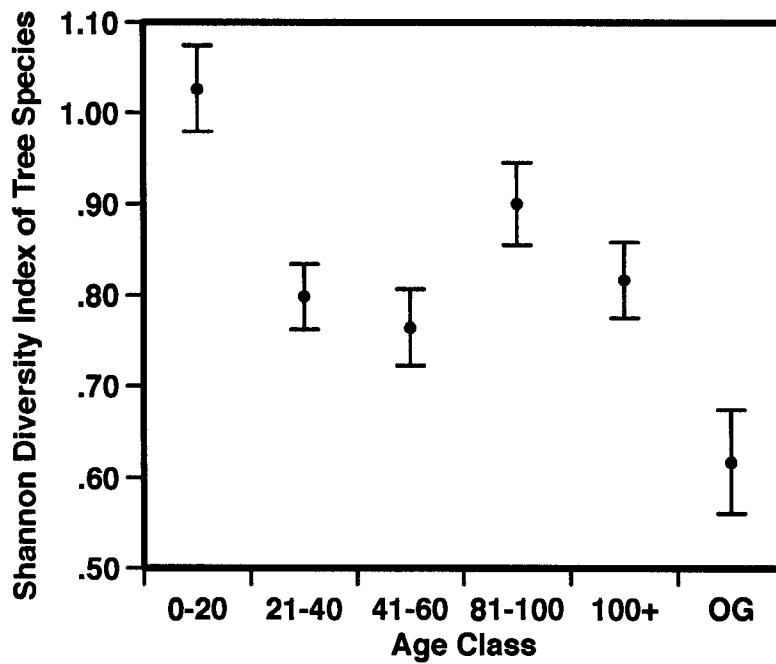


Figure 8. One-Way ANOVA between mean Shannon-Weiner Diversity Index of tree species and age class in regenerating and old-growth forests.

Table 4. Mean Shannon-Weiner Diversity Index of tree species post hoc comparisons.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.229	3.806	< 0.001	Yes
0-20 - 41-60	0.263	4.106	< 0.001	Yes
0-20 - 81-100	0.127	1.913	0.058	No
0-20 - 100+	0.210	3.290	0.001	Yes
0-20 - OG	0.410	5.514	< 0.001	Yes
21-40 - 41-60	0.034	0.610	> 0.5	No
21-40 - 81-100	-0.102	1.768	0.080	No
21-40 - 100+	-0.018	0.331	> 0.5	No
21-40 - OG	0.181	2.702	0.008	No
41-60 - 81-100	-0.136	2.201	0.030	No
41-60 - 100+	-0.052	0.876	0.383	No
41-60 - OG	0.147	2.091	0.039	No
81-100 - 100+	0.084	1.357	0.177	No
81-100 - OG	0.283	3.909	< 0.001	Yes
100+ - OG	0.200	2.829	0.005	No



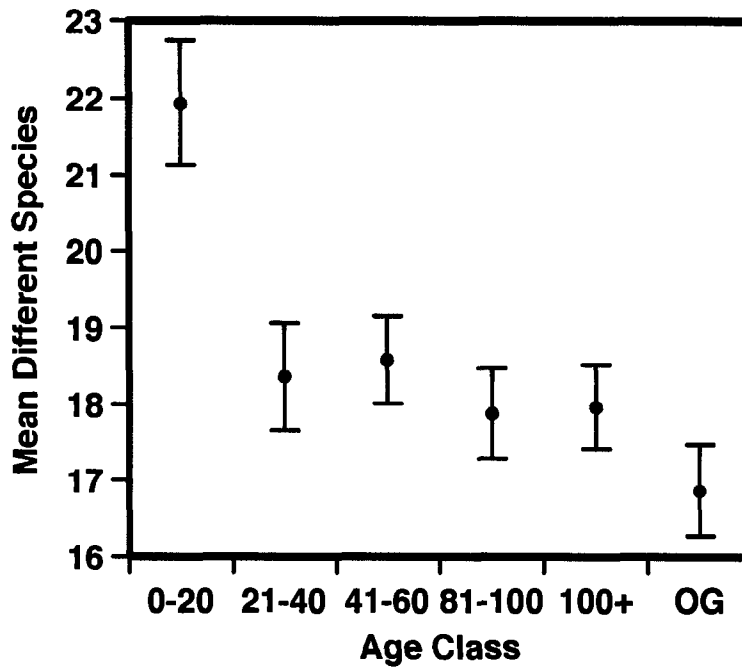


Figure 9. One-Way ANOVA between mean species richness and age class in regenerating and old-growth forests.

Table 5. Mean species richness post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	3.567	3.330	0.001	Yes
0-20 - 41-60	3.350	3.395	< 0.001	Yes
0-20 - 81-100	4.050	4.033	< 0.001	Yes
0-20 - 100+	3.967	4.064	< 0.001	Yes
0-20 - OG	5.067	5.017	< 0.001	Yes
21-40 - 41-60	-0.217	0.240	> 0.5	No
21-40 - 81-100	0.483	0.525	> 0.5	No
21-40 - 100+	0.400	0.449	> 0.5	No
21-40 - OG	1.500	1.617	0.108	No
41-60 - 81-100	0.700	0.852	0.396	No
41-60 - 100+	0.617	0.784	0.435	No
41-60 - OG	1.717	2.072	0.040	No
81-100 - 100+	-0.083	0.103	> 0.5	No
81-100 - OG	1.017	1.197	0.234	No
100+ - OG	1.100	1.349	0.180	No

### *Tree Species Parameters*

**Basal Area.** Dominance, or basal area, of tree species increased significantly as time since clearcut harvest increased. A One-Way ANOVA showed a significant change in total basal area over time ( $F(5, 360)=167.158, p<0.001$ ) (Figure 10). Additional analysis illustrated that specific age classes differed from one another (Table 6). A significant positive linear regression between total basal area and time since harvest ( $y = 0.829x + 7.400$ ) supported these results ( $p<0.001, r^2=0.394$ ). The basal area of specific tree species also significantly changed. A One-Way ANOVA illustrated the dramatic increase in *Sequoia sempervirens* basal area ( $F(5, 360)=81.207, p<0.001$ ) (Figure 11). Basal area of *S. sempervirens* illustrated differences between age classes as well (Table 7). A One-Way ANOVA indicated *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir) was slightly lower in old-growth forests ( $F(5, 360)=8.280, p<0.001$ ) (Figure 12). Post hoc analysis between mean Douglas-fir basal area and age class yielded significant results (Table 8).

A One-Way ANOVA illustrated a sharp decrease in *Lithocarpus densiflorus* (tanoak) in old-growth forests compared to mature regenerating redwood forests ( $F(5, 360)=28.822, p<0.001$ ) (Figure 13). Additional comparisons illustrated a significant difference in tanoak basal area and age class (Table 9). Basal area of *Tsuga heterophylla* (western hemlock) increased strongly over time after harvest but was slightly lower in old-growth sites ( $F(5, 360)=7.372, p<0.001$ ) (Figure 14). Additional analysis illustrated a significant difference in mean hemlock basal area between age classes (Table 10).

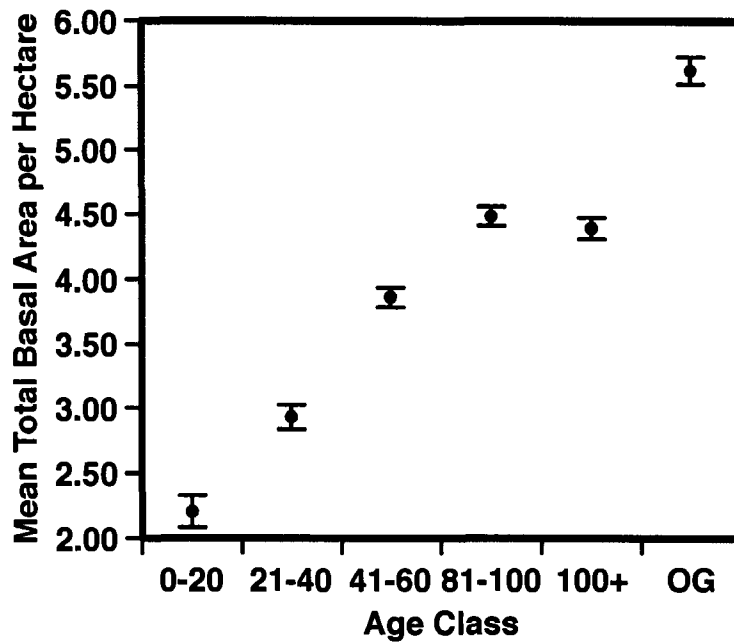


Figure 10. One-Way ANOVA between mean dominance and age class in regenerating and old-growth forests.

Table 6. Mean tree species dominance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-0.720	4.671	< 0.001	Yes
0-20 - 41-60	-1.652	11.404	< 0.001	Yes
0-20 - 81-100	-2.272	15.931	< 0.001	Yes
0-20 - 100+	-2.180	14.678	< 0.001	Yes
0-20 - OG	-3.413	21.336	< 0.001	Yes
21-40 - 41-60	-0.933	7.683	< 0.001	Yes
21-40 - 81-100	-1.553	13.080	< 0.001	Yes
21-40 - 100+	-1.460	11.616	< 0.001	Yes
21-40 - OG	-2.693	19.370	< 0.001	Yes
41-60 - 81-100	-0.620	5.823	< 0.001	Yes
41-60 - 100+	-0.527	4.617	< 0.001	Yes
41-60 - OG	-1.761	13.672	< 0.001	Yes
81-100 - 100+	0.093	0.833	0.406	No
81-100 - OG	-1.141	9.033	< 0.001	Yes
100+ - OG	-1.233	9.284	< 0.001	Yes

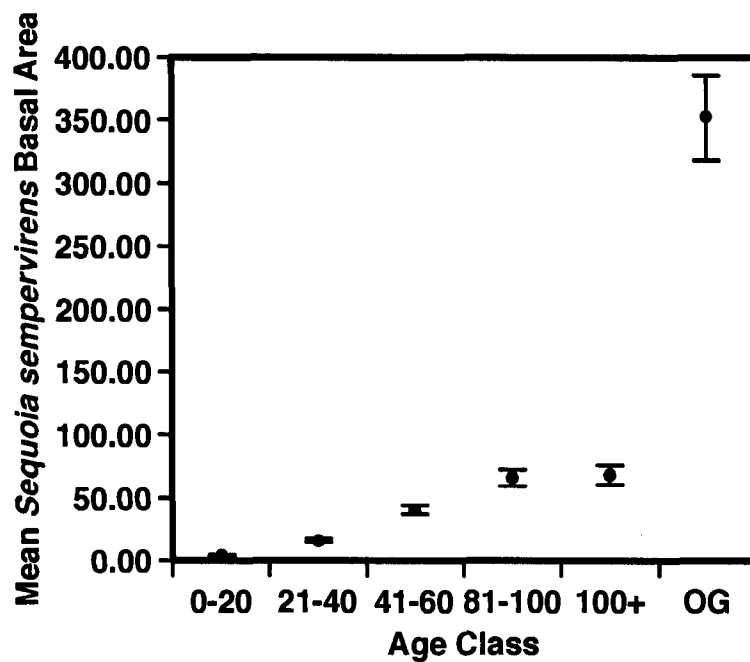


Figure 11. One-Way ANOVA between mean *Sequoia sempervirens* dominance and age class in regenerating and old-growth forests.

Table 7. Mean *S. sempervirens* dominance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-11.603	6.970	< 0.001	Yes
0-20 - 41-60	-36.372	9.562	< 0.001	Yes
0-20 - 81-100	-62.045	9.738	< 0.001	Yes
0-20 - 100+	-64.411	8.385	< 0.001	Yes
0-20 - OG	-347.718	10.298	< 0.001	Yes
21-40 - 41-60	-24.769	6.143	< 0.001	Yes
21-40 - 81-100	-50.443	7.748	< 0.001	Yes
21-40 - 100+	-52.808	6.773	< 0.001	Yes
21-40 - OG	-336.116	9.947	< 0.001	Yes
41-60 - 81-100	-25.674	3.491	< 0.001	Yes
41-60 - 100+	-28.039	3.293	0.001	Yes
41-60 - OG	-311.347	9.167	< 0.001	Yes
81-100 - 100+	-2.366	0.238	> 0.5	No
81-100 - OG	-285.673	8.317	< 0.001	Yes
100+ - OG	-283.307	8.185	< 0.001	Yes

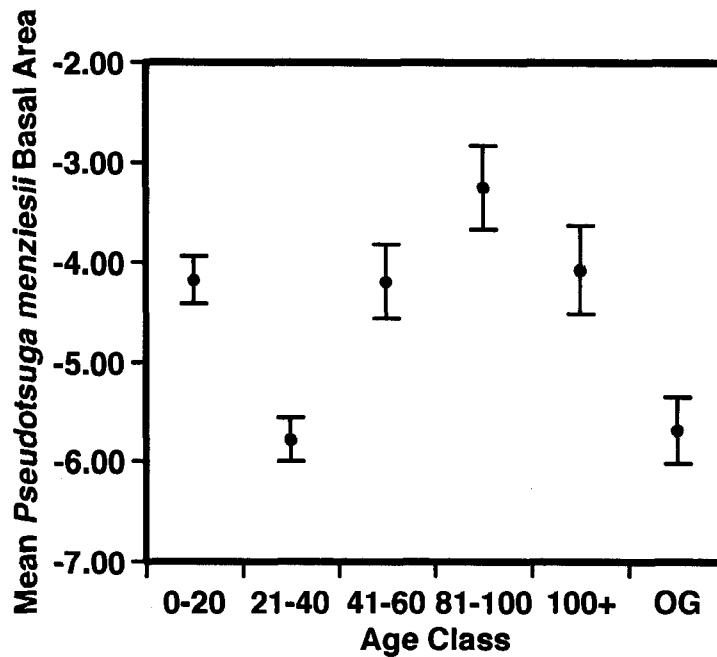


Figure 12. One-Way ANOVA between mean *P. menziesii* var. *menziesii* dominance and age class in regenerating and old-growth forests.

Table 8. Mean *Pseudotsuga menziesii* var. *menziesii* dominance post hoc comparisons.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	1.608	4.983	< 0.001	Yes
0-20 - 41-60	0.013	0.031	> 0.5	No
0-20 - 81-100	-0.919	1.907	0.059	No
0-20 - 100+	-0.099	0.198	> 0.5	No
0-20 - OG	1.511	3.668	< 0.001	Yes
21-40 - 41-60	-1.594	3.715	< 0.001	Yes
21-40 - 81-100	-2.527	5.339	< 0.001	Yes
21-40 - 100+	-1.707	3.488	< 0.001	Yes
21-40 - OG	-0.097	0.240	> 0.5	No
41-60 - 81-100	-0.932	1.668	0.098	No
41-60 - 100+	-0.112	0.196	> 0.5	No
41-60 - OG	1.498	2.996	0.003	Yes
81-100 - 100+	0.820	1.353	0.179	No
81-100 - OG	2.430	4.515	< 0.001	Yes
100+ - OG	1.610	2.915	0.004	No

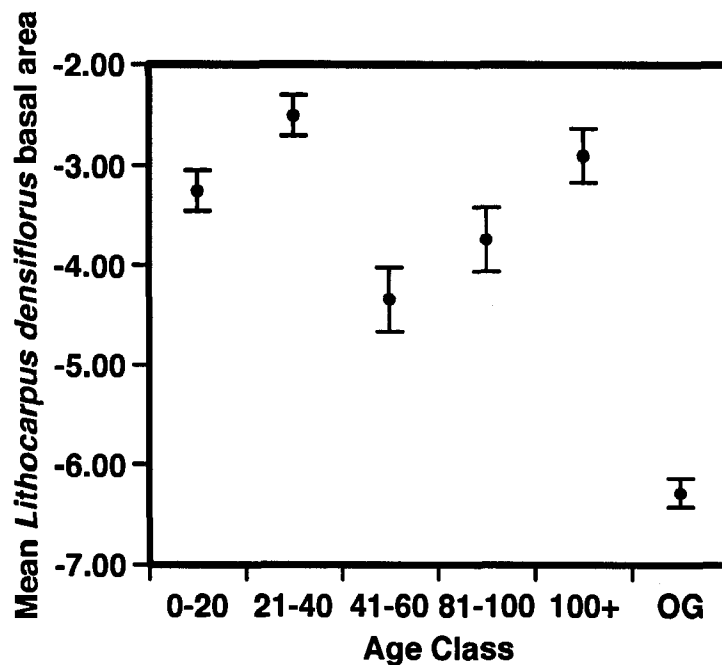


Figure 13. One-Way ANOVA between mean *Lithocarpus densiflorus* dominance and age class in regenerating and old-growth forests.

Table 9. Mean *L. densiflorus* dominance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-0.749	2.631	0.010	No
0-20 - 41-60	1.095	2.850	0.005	No
0-20 - 81-100	0.488	1.280	0.203	No
0-20 - 100+	-0.347	1.021	0.309	No
0-20 - OG	3.031	12.261	< 0.001	Yes
21-40 - 41-60	1.844	4.829	< 0.001	Yes
21-40 - 81-100	1.237	3.263	0.001	Yes
21-40 - 100+	0.402	1.193	0.235	No
21-40 - OG	3.780	15.523	< 0.001	Yes
41-60 - 81-100	-0.607	1.323	0.188	No
41-60 - 100+	-1.442	3.397	< 0.001	Yes
41-60 - OG	1.936	5.457	< 0.001	Yes
81-100 - 100+	-0.835	1.979	0.050	No
81-100 - OG	2.543	7.228	< 0.001	Yes
100+ - OG	3.378	11.041	< 0.001	Yes

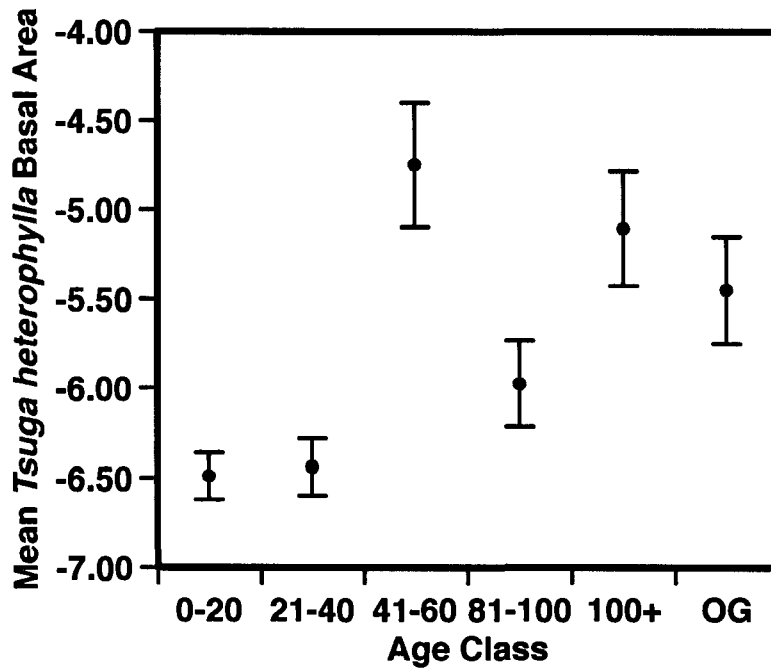


Figure 14. One-Way ANOVA between mean *Tsuga heterophylla* dominance and age class in regenerating and old-growth forests.

Table 10. Mean *T. heterophylla* dominance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-0.050	0.241	> 0.5	No
0-20 - 41-60	-1.739	4.646	< 0.001	Yes
0-20 - 81-100	-0.513	1.860	0.065	No
0-20 - 100+	-1.382	3.975	< 0.001	Yes
0-20 - OG	-1.038	3.180	0.002	Yes
21-40 - 41-60	-1.689	4.386	< 0.001	Yes
21-40 - 81-100	-0.463	1.595	0.113	No
21-40 - 100+	-1.332	3.707	< 0.001	Yes
21-40 - OG	-0.988	2.917	0.004	No
41-60 - 81-100	1.226	2.880	0.005	No
41-60 - 100+	0.357	0.751	0.454	No
41-60 - OG	0.701	1.523	0.130	No
81-100 - 100+	-0.869	2.159	0.033	No
81-100 - OG	-0.525	1.366	0.174	No
100+ - OG	0.344	0.783	0.435	No

*Importance.* Importance Value, the summation of relative dominance, relative density, and relative frequency, is a value used to indicate the overall significance of a species. A few species increased in Importance Value with age from harvest. *Sequoia sempervirens* was very important in old-growth forests ( $F(5, 360)=28.615, p<0.001$ ) (Figure 15). Additional analysis indicated redwood also differed between age classes (Table 11). Importance of *Tsuga heterophylla* (western hemlock) typically increased with age in regenerating stands and was important in old-growth stands ( $F(5, 360)=4.225, p<0.001$ ) (Figure 16). Post hoc analysis between hemlock importance and age class were also significant (Table 12).

The change in Importance Value of other species differed. *Umbellularia californica* (California bay) initially decreased, but increased in later stages of development ( $F(5, 360)=7.231, p<0.001$ ) (Figure 17). The bimodal pattern of development of California bay was unique among the tree species sampled. Additional analysis between age classes and California bay importance illustrated significant differences (Table 13). A One-Way ANOVA between *Lithocarpus densiflorus* (tanoak) and time revealed tanoak importance was much lower in old-growth forests ( $F(5, 360)=23.167, p<0.001$ ) (Figure 18). *L. densiflorus* also significantly differed between age groups (Table 14). *Abies grandis* (grand fir) exhibited a significant change over time and was less important in old-growth ( $F(5, 360)=10.806, p<0.001$ ) (Figure 19). Post hoc analysis between grand fir importance and age class was also significant (Table 15).



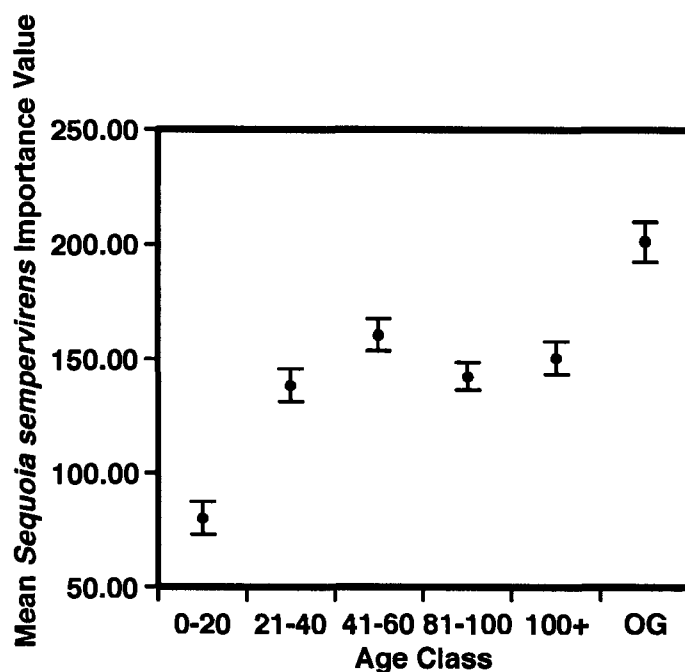


Figure 15. One-Way ANOVA between mean *Sequoia sempervirens* importance and age class in regenerating and old-growth forests.

Table 11. Mean *S. sempervirens* importance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-58.118	5.570	< 0.001	Yes
0-20 - 41-60	-80.605	7.821	< 0.001	Yes
0-20 - 81-100	-62.185	6.616	< 0.001	Yes
0-20 - 100+	-70.512	6.904	< 0.001	Yes
0-20 - OG	-121.547	10.680	< 0.001	Yes
21-40 - 41-60	-22.487	2.154	0.033	No
21-40 - 81-100	-4.068	0.426	> 0.5	No
21-40 - 100+	-12.395	1.198	0.233	No
21-40 - OG	-63.429	5.516	< 0.001	Yes
41-60 - 81-100	18.419	1.958	0.053	No
41-60 - 100+	10.092	0.988	0.325	No
41-60 - OG	-40.943	3.596	< 0.001	Yes
81-100 - 100+	-8.327	0.895	0.373	No
81-100 - OG	-59.362	5.616	< 0.001	Yes
100+ - OG	-51.035	4.516	< 0.001	Yes

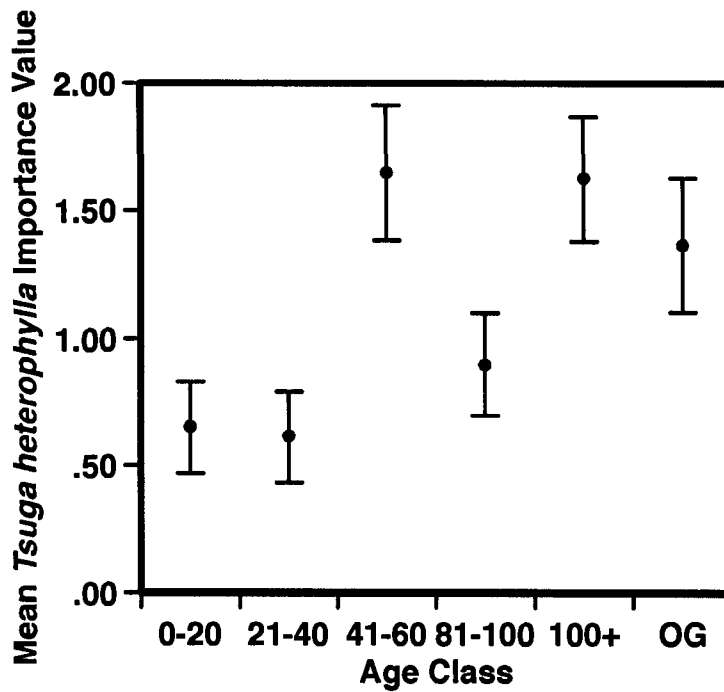


Figure 16. One-Way ANOVA between mean *Tsuga heterophylla* importance and age class in regenerating and old-growth forests.

Table 12. Mean *T. heterophylla* importance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.038	0.150	> 0.5	No
0-20 - 41-60	-0.997	3.117	0.002	Yes
0-20 - 81-100	-0.247	0.909	0.365	No
0-20 - 100+	-0.974	3.209	0.002	Yes
0-20 - OG	-0.714	2.242	0.027	No
21-40 - 41-60	-1.036	3.246	0.002	Yes
21-40 - 81-100	-0.286	1.054	0.294	No
21-40 - 100+	-1.013	3.345	0.001	Yes
21-40 - OG	-0.752	2.369	0.019	No
41-60 - 81-100	0.750	2.253	0.026	No
41-60 - 100+	0.023	0.064	> 0.5	No
41-60 - OG	0.284	0.763	0.447	No
81-100 - 100+	-0.727	2.292	0.024	No
81-100 - OG	-0.466	1.407	0.162	No
100+ - OG	0.261	0.729	0.468	No

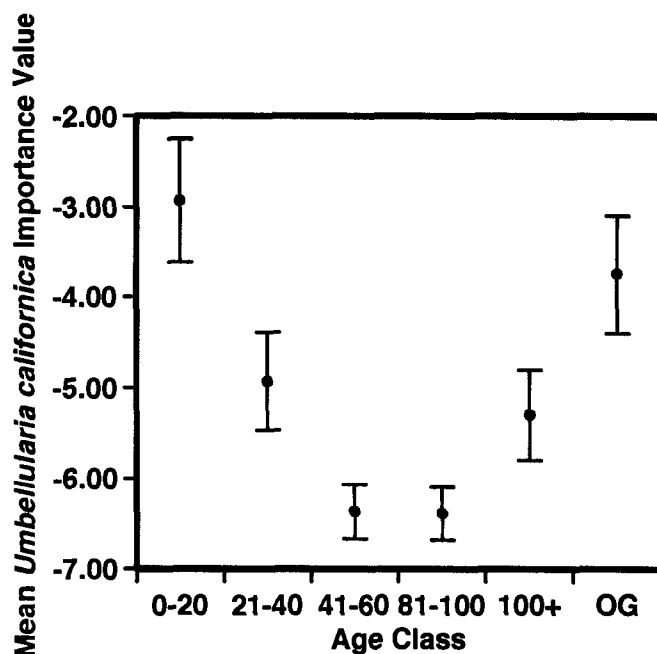


Figure 17. One-Way ANOVA between mean *Umbellularia californica* importance and age class in regenerating and old-growth forests.

Table 13. Mean *U. californica* importance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	2.000	2.291	0.024	No
0-20 - 41-60	3.439	4.598	< 0.001	Yes
0-20 - 81-100	3.463	4.663	< 0.001	Yes
0-20 - 100+	2.371	2.805	0.006	No
0-20 - OG	0.816	0.863	0.390	No
21-40 - 41-60	1.439	2.308	0.023	No
21-40 - 81-100	1.463	2.370	0.019	No
21-40 - 100+	0.371	0.503	> 0.5	No
21-40 - OG	-1.183	1.390	0.167	No
41-60 - 81-100	0.024	0.056	> 0.5	No
41-60 - 100+	-1.069	1.829	0.070	No
41-60 - OG	-2.623	3.629	< 0.001	Yes
81-100 - 100+	-1.092	1.892	0.061	No
81-100 - OG	-2.646	3.690	< 0.001	Yes
100+ - OG	-1.554	1.889	0.061	No

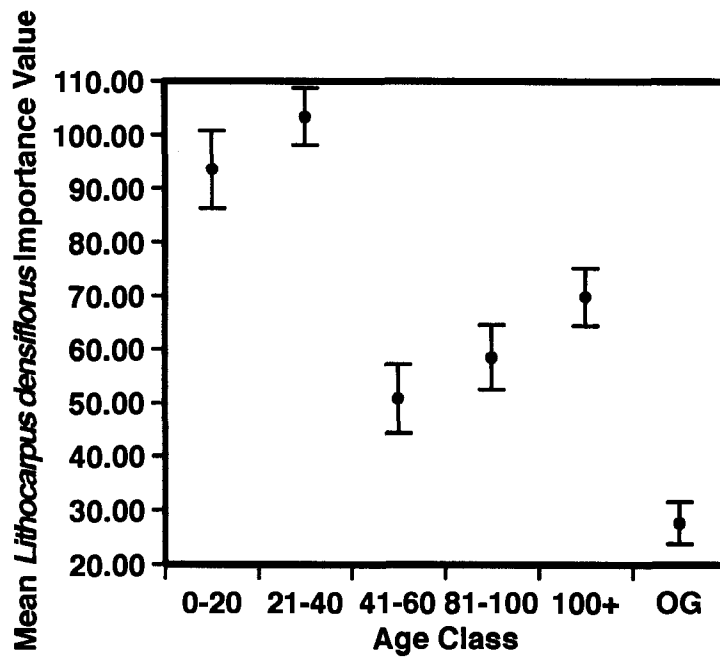


Figure 18. One-Way ANOVA between mean *Lithocarpus densiflorus* importance and age class in regenerating and old-growth forests.

Table 14. Mean *L. densiflorus* importance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-9.906	1.102	0.273	No
0-20 - 41-60	42.845	4.402	< 0.001	Yes
0-20 - 81-100	35.057	3.720	< 0.001	Yes
0-20 - 100+	23.738	2.624	0.010	No
0-20 - OG	65.866	8.014	< 0.001	Yes
21-40 - 41-60	52.751	6.288	< 0.001	Yes
21-40 - 81-100	44.963	5.601	< 0.001	Yes
21-40 - 100+	33.644	4.439	< 0.001	Yes
21-40 - OG	75.772	11.530	< 0.001	Yes
41-60 - 81-100	-7.788	0.880	0.381	No
41-60 - 100+	-19.108	2.263	0.025	No
41-60 - OG	23.021	3.048	0.003	Yes
81-100 - 100+	-11.319	1.400	0.164	No
81-100 - OG	30.809	4.309	< 0.001	Yes
100+ - OG	42.129	6.343	< 0.001	Yes

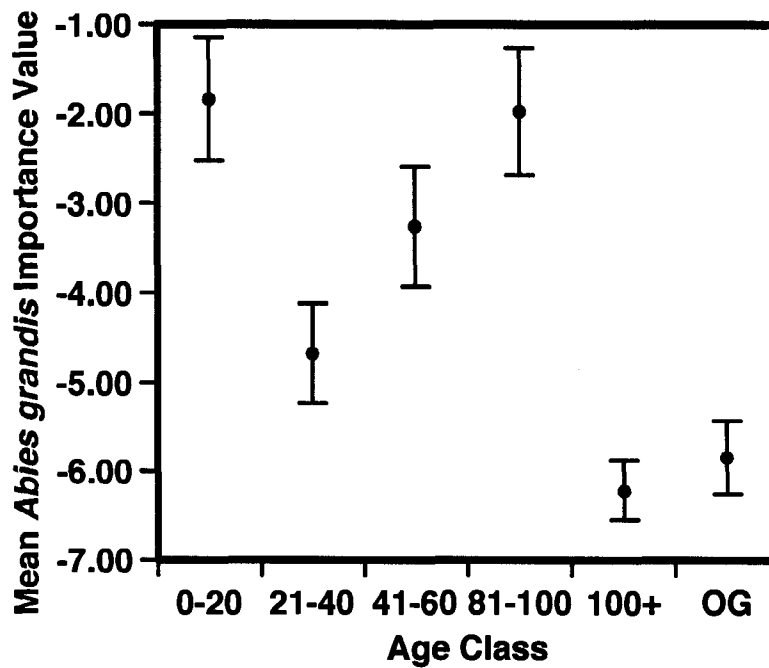


Figure 19. One-Way ANOVA between mean *Abies grandis* importance and age class in regenerating and old-growth forests.

Table 15. Mean *Abies grandis* importance post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	2.845	3.234	0.002	Yes
0-20 - 41-60	1.428	1.489	0.139	No
0-20 - 81-100	0.135	0.136	> 0.5	No
0-20 - 100+	4.387	5.755	< 0.001	Yes
0-20 - OG	4.014	5.015	< 0.001	Yes
21-40 - 41-60	-1.416	1.628	0.106	No
21-40 - 81-100	-2.710	3.007	0.003	Yes
21-40 - 100+	1.542	2.385	0.019	No
21-40 - OG	1.169	1.692	0.093	No
41-60 - 81-100	-1.293	1.321	0.189	No
41-60 - 100+	2.959	3.939	< 0.001	Yes
41-60 - OG	2.586	3.274	0.001	Yes
81-100 - 100+	4.252	5.402	< 0.001	Yes
81-100 - OG	3.879	4.707	< 0.001	Yes
100+ - OG	-0.373	0.699	0.486	No

### *Understory Parameters*

Several understory parameters significantly changed with time after clearcut harvest. A One-Way ANOVA illustrated an initial decrease in overall cover followed by an increase and high levels in old-growth stands ( $F(5, 360)=52.140, p<0.001$ ) (Figure 20). Additional analysis illustrated a significant difference in cover between age classes (Table 16). Herbaceous cover illustrated a similar pattern with much higher cover in old-growth stands versus all other age classes ( $F(5, 360)=35.366, p<0.001$ ) (Figure 21). Detailed analysis of herb cover between age classes also yielded significance (Table 17).

Diversity of understory species changed significantly in regenerating forests in contrast to old-growth forests. The Shannon-Weiner Diversity Index ( $F(5, 360)=5.430, p<0.001$ ) (Figure 22) and richness of understory species ( $F(5, 360)=4.261, p<0.001$ ) (Figure 23) were lower in old-growth forests. Post hoc analysis of understory diversity (Table 18) and understory richness (Table 19) illustrated significant differences among age groups. Relative distribution of understory species (evenness) also exhibited a similar pattern of development that was significant overall ( $F(5, 360)=7.238, p<0.001$ ) (Figure 24) and between specific age classes (Table 20).

Cover of exotic species changed significantly with time from clearcut harvest. All exotic species sampled were herbaceous and cover was significantly lower in 41-60 year stands compared to 0-20 or 21-40 year stands ( $F(5, 360)=16.328, p<0.001$ ) (Figure 25). Exotic species were absent in stands older than 60 years and in old-growth stands. Additional analysis indicated significant differences between stand age (Table 21).

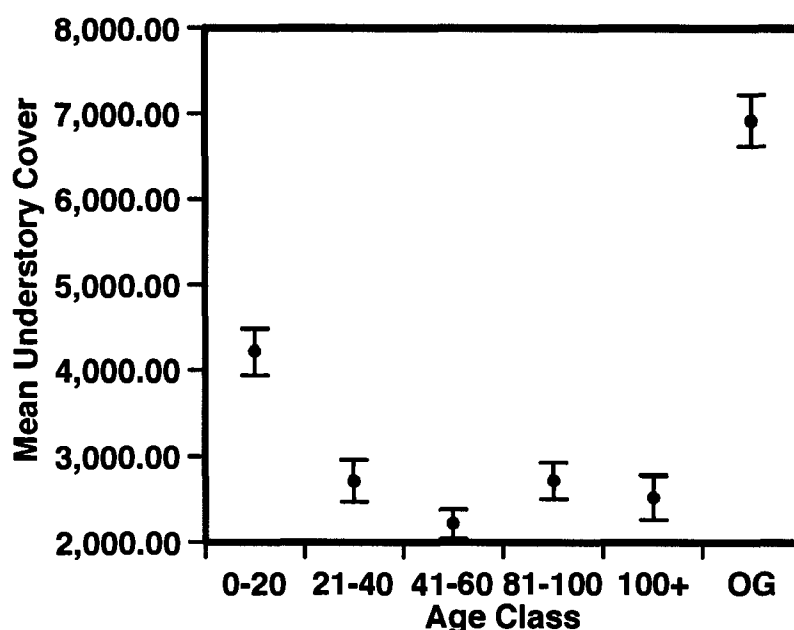


Figure 20. One-Way ANOVA between mean understory species cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 16. Mean understory species cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	1493.167	4.062	< 0.001	Yes
0-20 - 41-60	1997.333	6.264	< 0.001	Yes
0-20 - 81-100	1489.500	4.332	< 0.001	Yes
0-20 - 100+	1688.167	4.466	< 0.001	Yes
0-20 - OG	-2711.333	6.675	< 0.001	Yes
21-40 - 41-60	504.167	1.683	0.095	No
21-40 - 81-100	-3.667	0.011	> 0.5	No
21-40 - 100+	195.000	0.539	> 0.5	No
21-40 - OG	-4204.500	10.745	< 0.001	Yes
41-60 - 81-100	-507.833	1.881	0.062	No
41-60 - 100+	-309.167	0.990	0.324	No
41-60 - OG	-4708.667	13.613	< 0.001	Yes
81-100 - 100+	198.667	0.588	> 0.5	No
81-100 - OG	-4200.833	11.382	< 0.001	Yes
100+ - OG	-4399.500	10.969	< 0.001	Yes

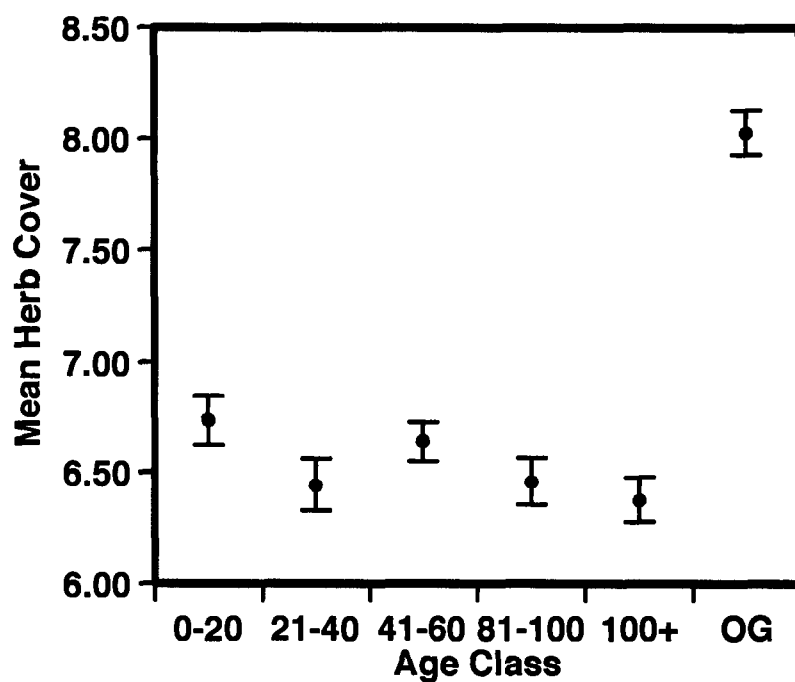


Figure 21. One-Way ANOVA between mean herbaceous species cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 17. Mean herbaceous species cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.290	1.792	0.076	No
0-20 - 41-60	0.095	0.672	> 0.5	No
0-20 - 81-100	0.275	1.793	0.076	No
0-20 - 100+	0.357	2.342	0.021	No
0-20 - OG	-1.293	8.547	< 0.001	Yes
21-40 - 41-60	-0.195	1.330	0.186	No
21-40 - 81-100	-0.015	0.092	> 0.5	No
21-40 - 100+	0.067	0.429	> 0.5	No
21-40 - OG	-1.583	10.155	< 0.001	Yes
41-60 - 81-100	0.180	1.313	0.192	No
41-60 - 100+	0.262	1.926	0.057	No
41-60 - OG	-1.388	10.302	< 0.001	Yes
81-100 - 100+	0.082	0.551	> 0.5	No
81-100 - OG	-1.569	10.644	< 0.001	Yes
100+ - OG	-1.650	11.283	< 0.001	Yes



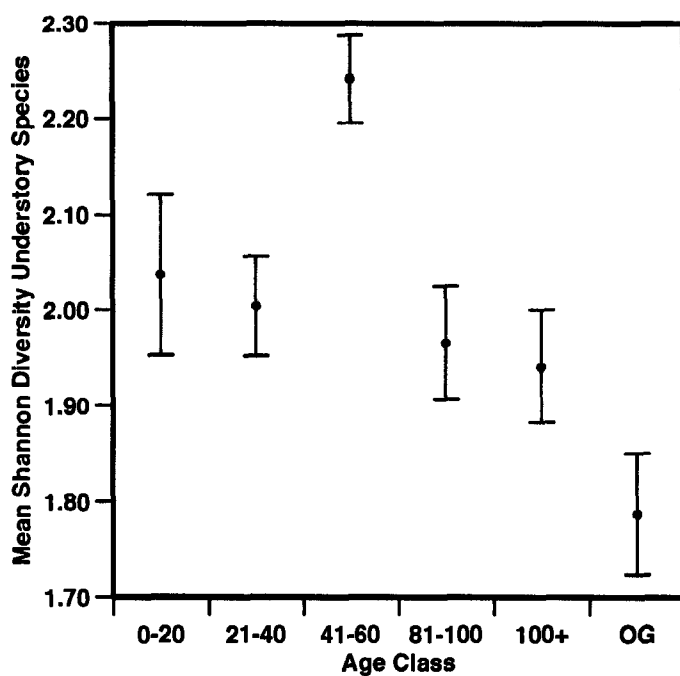


Figure 22. One-Way ANOVA between mean Shannon-Weiner Diversity Index of understory species and age class in regenerating and old-growth forests.

Table 18. Mean Shannon-Weiner Diversity Index of understory post hoc comparisons.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.033	0.332	> 0.5	No
0-20 - 41-60	-0.204	2.135	0.035	No
0-20 - 81-100	0.071	0.692	0.490	No
0-20 - 100+	0.096	0.936	0.351	No
0-20 - OG	0.251	2.379	0.019	No
21-40 - 41-60	-0.237	3.432	< 0.001	Yes
21-40 - 81-100	0.038	0.486	> 0.5	No
21-40 - 100+	0.063	0.806	0.422	No
21-40 - OG	0.218	2.656	0.009	No
41-60 - 81-100	0.275	3.684	< 0.001	Yes
41-60 - 100+	0.300	4.032	< 0.001	Yes
41-60 - OG	0.455	5.825	< 0.001	Yes
81-100 - 100+	0.025	0.299	> 0.5	No
81-100 - OG	0.179	2.066	0.041	No
100+ - OG	0.154	1.783	0.077	No

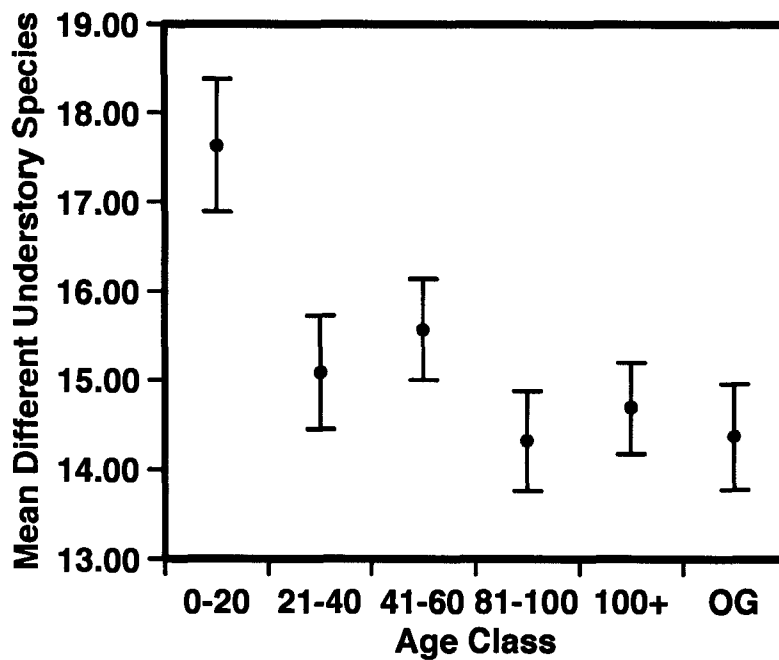


Figure 23. One-Way ANOVA between mean understory species richness and age class in regenerating and old-growth forests.

Table 19. Mean understory species richness post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	2.550	2.599	0.011	No
0-20 - 41-60	2.067	2.215	0.029	No
0-20 - 81-100	3.317	3.586	< 0.001	Yes
0-20 - 100+	2.950	3.287	0.001	Yes
0-20 - OG	3.267	3.466	< 0.001	Yes
21-40 - 41-60	-0.483	0.563	> 0.5	No
21-40 - 81-100	0.767	0.902	0.369	No
21-40 - 100+	0.400	0.488	> 0.5	No
21-40 - OG	0.717	0.825	0.411	No
41-60 - 81-100	1.250	1.574	0.118	No
41-60 - 100+	0.883	1.160	0.249	No
41-60 - OG	1.200	1.474	0.143	No
81-100 - 100+	-0.367	0.488	> 0.5	No
81-100 - OG	-0.050	0.062	> 0.5	No
100+ - OG	0.317	0.410	> 0.5	No

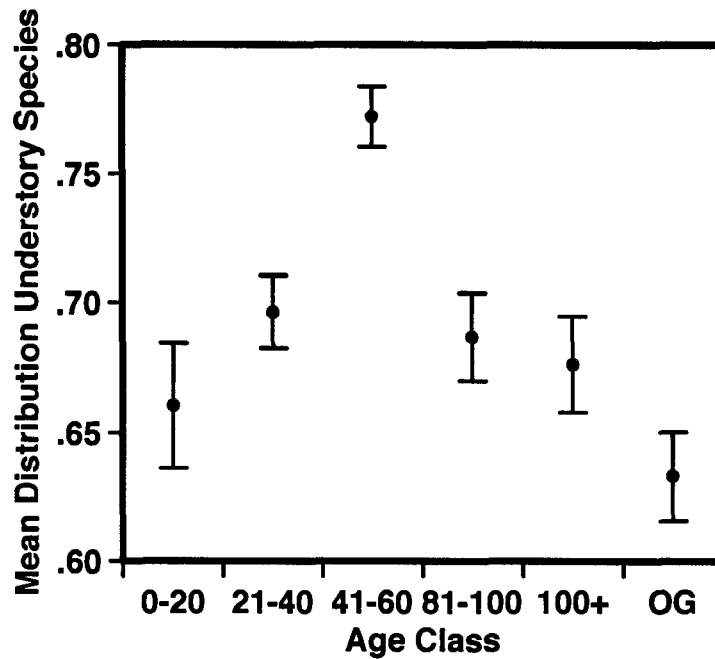


Figure 24. One-Way ANOVA between mean understory species evenness and age class in regenerating and old-growth forests.

Table 20. Mean understory species evenness post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-0.036	1.293	0.198	No
0-20 - 41-60	-0.112	4.172	< 0.001	Yes
0-20 - 81-100	-0.027	0.901	0.369	No
0-20 - 100+	-0.016	0.526	> 0.5	No
0-20 - OG	0.027	0.921	0.359	No
21-40 - 41-60	-0.076	4.151	< 0.001	Yes
21-40 - 81-100	0.010	0.438	> 0.5	No
21-40 - 100+	0.020	0.870	0.386	No
21-40 - OG	0.064	2.846	0.005	No
41-60 - 81-100	0.085	4.167	< 0.001	Yes
41-60 - 100+	0.096	4.398	< 0.001	Yes
41-60 - OG	0.139	6.661	< 0.001	Yes
81-100 - 100+	0.011	0.423	> 0.5	No
81-100 - OG	0.054	2.230	0.028	No
100+ - OG	0.043	1.713	0.089	No

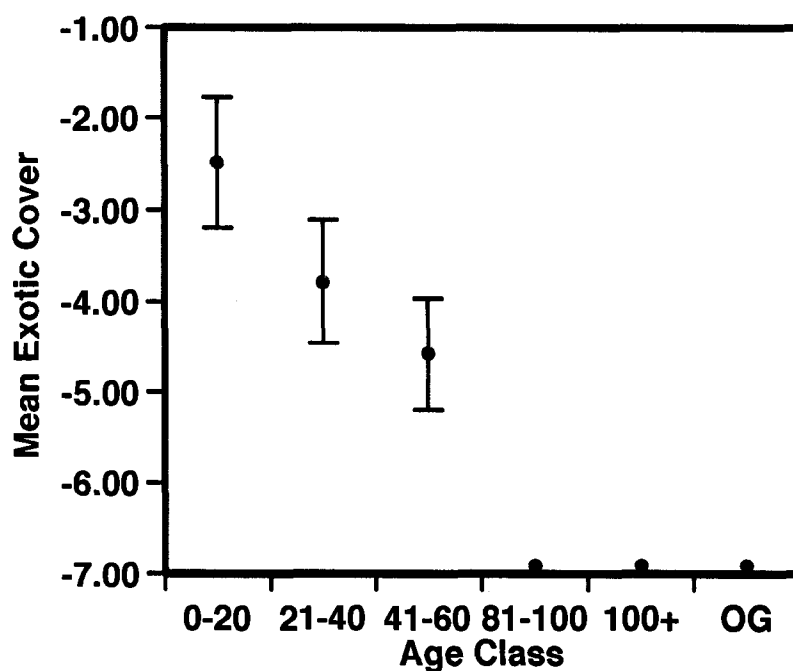


Figure 25. One-Way ANOVA between mean exotic species cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 21. Mean exotic species cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	1.303	1.329	0.186	No
0-20 - 41-60	2.093	2.236	0.027	No
0-20 - 81-100	4.422	6.230	< 0.001	Yes
0-20 - 100+	4.422	6.230	< 0.001	Yes
0-20 - OG	4.422	6.230	< 0.001	Yes
21-40 - 41-60	0.790	0.867	0.387	No
21-40 - 81-100	3.119	4.613	< 0.001	Yes
21-40 - 100+	3.119	4.613	< 0.001	Yes
21-40 - OG	3.119	4.613	< 0.001	Yes
41-60 - 81-100	2.329	3.820	< 0.001	Yes
41-60 - 100+	2.329	3.820	< 0.001	Yes
41-60 - OG	2.329	3.820	< 0.001	Yes
81-100 - 100+	0.000	0.000	> 0.5	No
81-100 - OG	0.000	0.000	> 0.5	No
100+ - OG	0.000	0.000	> 0.5	No

### *Understory Species Parameters*

Specific understory species also changed after clearcut harvest. *Trillium ovatum* (Pacific trillium) significantly increased and exhibited higher cover in old-growth stands ( $F(5, 360)=16.247, p<0.001$ ) (Figure 26). Post hoc analysis illustrated significant differences between age classes (Table 22). The One-Way ANOVA between mean *Tiarella trifoliata* var. *unifoliata* (sugar scoop) cover and age class exhibited similar a priori results ( $F(5, 360)=36.527, p<0.001$ ) (Figure 27) and post hoc results (Table 23). *Viola sempervirens* (redwood violet) also increased in a similar way, was higher in old-growth stands ( $F(5, 360)=2.566, p=0.027$ ) (Figure 28), and differed between age classes (Table 24). *Oxalis oregana* (redwood sorrel) illustrated a bimodal pattern of development after clearcut harvest. *O. oregana* slowly increased in regenerating stands and was higher in old-growth stands ( $F(5, 360)=11.937, p<0.001$ ) (Figure 29). *O. oregana* yielded significant results when specific age class means were compared (Table 25).

Shrub species, such as *Gaultheria shallon* (salal), significantly changed. Salal increased and was highest in old-growth stands ( $F(5, 360)=5.063, p<0.001$ ) (Figure 30). Further analysis indicated specific age classes differed (Table 26). *Rhododendron macrophyllum* (California rhododendron) significantly changed ( $F(5, 360)=4.758, p<0.001$ ) (Figure 31) and illustrated differences between means of age classes (Table 27). *Toxicodendron diversilobum* (poison oak) decreased initially, but demonstrated an increase in older stands ( $F(5, 360)=12.900, p<0.001$ ) (Figure 32). The bimodal distribution of *T. diversilobum* was apparent in the post hoc comparisons (Table 28).

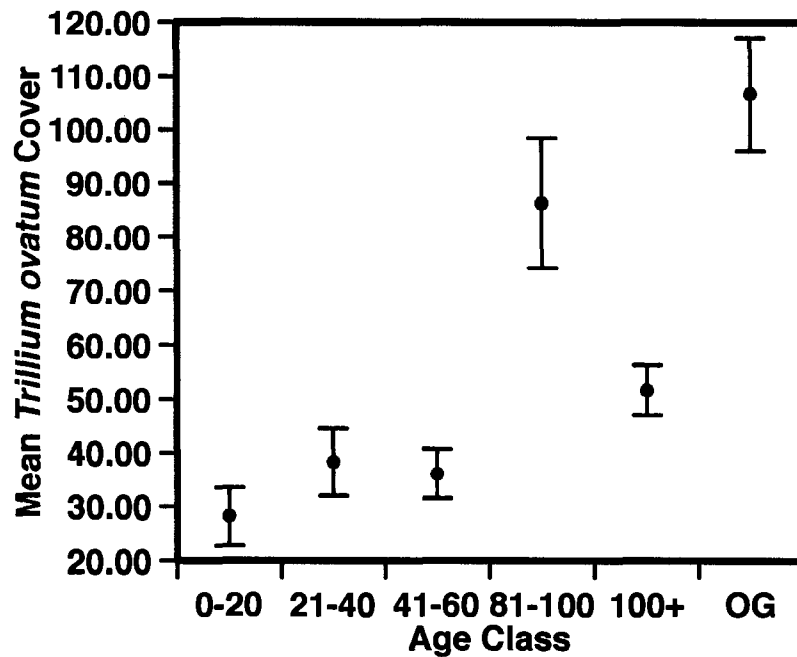


Figure 26. One-Way ANOVA between mean *Trillium ovatum* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 22. Mean *Trillium ovatum* cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-10.167	1.227	0.222	No
0-20 - 41-60	-8.000	1.130	0.261	No
0-20 - 81-100	-58.167	4.399	< 0.001	Yes
0-20 - 100+	-23.500	3.332	0.001	Yes
0-20 - OG	-78.500	6.634	< 0.001	Yes
21-40 - 41-60	2.167	0.279	> 0.5	No
21-40 - 81-100	-48.000	3.528	< 0.001	Yes
21-40 - 100+	-13.333	1.720	0.088	No
21-40 - OG	-68.333	5.573	< 0.001	Yes
41-60 - 81-100	-50.167	3.887	< 0.001	Yes
41-60 - 100+	-15.500	2.405	0.018	No
41-60 - OG	-70.500	6.141	< 0.001	Yes
81-100 - 100+	34.667	2.689	0.008	No
81-100 - OG	-20.333	1.270	0.207	No
100+ - OG	-55.000	4.798	< 0.001	Yes

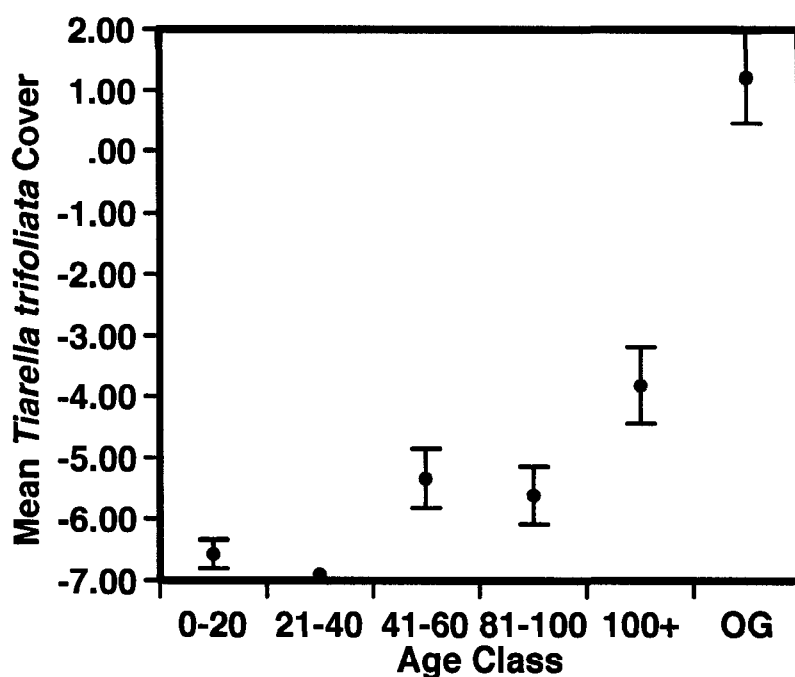


Figure 27. One-Way ANOVA between mean *Tiarella trifoliata* var. *unifoliata* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 23. Mean *T. trifoliata* var. *unifoliata* cover post hoc comparisons between ages.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.334	1.422	0.158	No
0-20 - 41-60	-1.235	2.283	0.024	No
0-20 - 81-100	-0.959	1.842	0.068	No
0-20 - 100+	-2.755	4.043	< 0.001	Yes
0-20 - OG	-7.792	9.881	< 0.001	Yes
21-40 - 41-60	-1.569	3.219	0.002	Yes
21-40 - 81-100	-1.293	2.782	0.006	No
21-40 - 100+	-3.089	4.828	< 0.001	Yes
21-40 - OG	-8.125	10.794	< 0.001	Yes
41-60 - 81-100	0.276	0.410	> 0.5	No
41-60 - 100+	-1.519	1.889	0.061	No
41-60 - OG	-6.556	7.310	< 0.001	Yes
81-100 - 100+	-1.795	2.270	0.025	No
81-100 - OG	-6.832	7.722	< 0.001	Yes
100+ - OG	-5.037	5.099	< 0.001	Yes

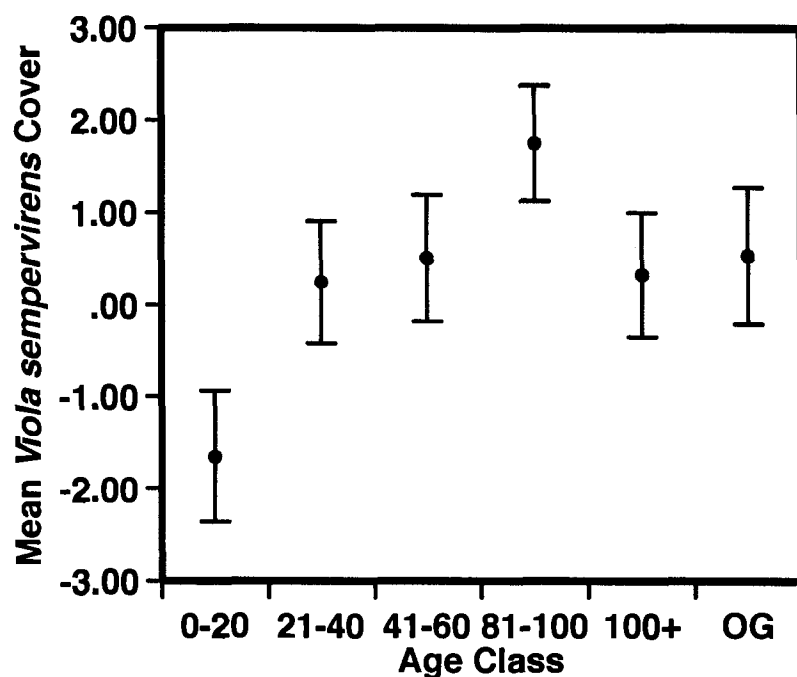


Figure 28. One-Way ANOVA between mean *Viola sempervirens* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 24. Mean *Viola sempervirens* cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-1.888	1.944	0.054	No
0-20 - 41-60	-2.153	2.183	0.031	No
0-20 - 81-100	-3.400	3.587	< 0.001	Yes
0-20 - 100+	-1.977	2.024	0.045	No
0-20 - OG	-2.177	2.125	0.036	No
21-40 - 41-60	-0.265	0.278	> 0.5	No
21-40 - 81-100	-1.512	1.653	0.101	No
21-40 - 100+	-0.088	0.094	> 0.5	No
21-40 - OG	-0.289	0.291	> 0.5	No
41-60 - 81-100	-1.247	1.340	0.183	No
41-60 - 100+	0.177	0.184	> 0.5	No
41-60 - OG	-0.024	0.024	> 0.5	No
81-100 - 100+	1.424	1.547	0.124	No
81-100 - OG	1.223	1.259	0.210	No
100+ - OG	-0.201	0.201	> 0.5	No



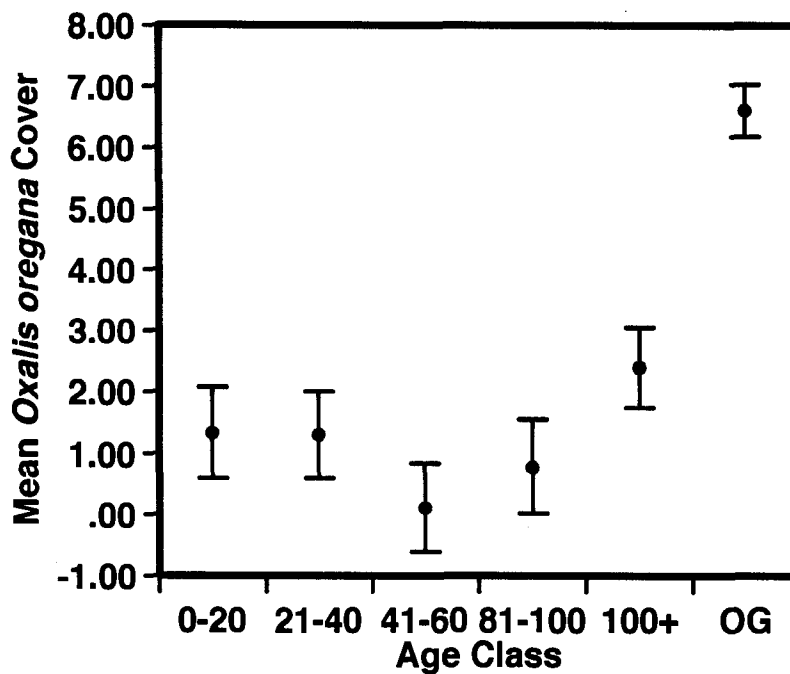


Figure 29. One-Way ANOVA between mean *Oxalis oregana* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 25. Mean *Oxalis oregana* cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.028	0.028	> 0.5	No
0-20 - 41-60	1.214	1.175	0.243	No
0-20 - 81-100	0.551	0.519	> 0.5	No
0-20 - 100+	-1.064	1.083	0.281	No
0-20 - OG	-5.286	6.211	< 0.001	Yes
21-40 - 41-60	1.186	1.175	0.242	No
21-40 - 81-100	0.523	0.504	> 0.5	No
21-40 - 100+	-1.092	1.141	0.256	No
21-40 - OG	-5.314	6.468	< 0.001	Yes
41-60 - 81-100	-0.662	0.628	> 0.5	No
41-60 - 100+	-2.278	2.337	0.021	No
41-60 - OG	-6.500	7.721	< 0.001	Yes
81-100 - 100+	-1.616	1.607	0.111	No
81-100 - OG	-5.837	6.655	< 0.001	Yes
100+ - OG	-4.222	5.419	< 0.001	Yes

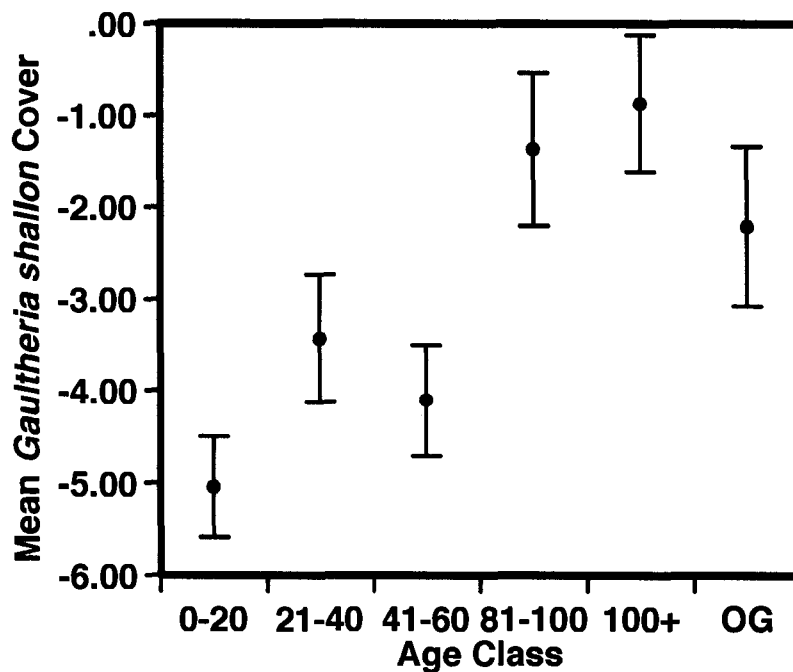


Figure 30. One-Way ANOVA between mean *Gaultheria shallon* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 26. Mean *Gaultheria shallon* cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	-1.614	1.832	0.069	No
0-20 - 41-60	-0.938	1.151	0.252	No
0-20 - 81-100	-3.678	3.707	< 0.001	Yes
0-20 - 100+	-4.174	4.525	< 0.001	Yes
0-20 - OG	-2.837	2.769	0.007	No
21-40 - 41-60	0.676	0.733	0.465	No
21-40 - 81-100	-2.064	1.908	0.059	No
21-40 - 100+	-2.560	2.514	0.013	No
21-40 - OG	-1.222	1.100	0.274	No
41-60 - 81-100	-2.740	2.664	0.009	No
41-60 - 100+	-3.236	3.366	0.001	Yes
41-60 - OG	-1.899	1.792	0.076	No
81-100 - 100+	-0.496	0.444	> 0.5	No
81-100 - OG	0.842	0.701	0.485	No
100+ - OG	1.338	1.169	0.245	No

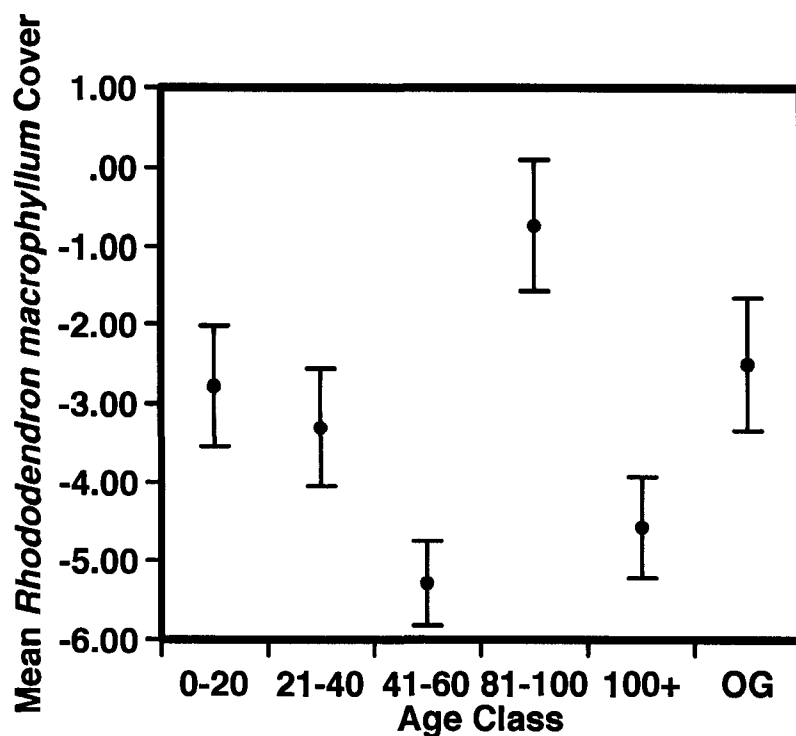


Figure 31. One-Way ANOVA between mean *Rhododendron macrophyllum* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 27. Mean *R. macrophyllum* cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	0.523	0.490	> 0.5	No
0-20 - 41-60	2.504	2.678	0.008	No
0-20 - 81-100	-2.043	1.804	0.074	No
0-20 - 100+	1.784	1.780	0.078	No
0-20 - OG	-0.283	0.249	> 0.5	No
21-40 - 41-60	1.981	2.149	0.034	No
21-40 - 81-100	-2.566	2.288	0.024	No
21-40 - 100+	1.261	1.274	0.205	No
21-40 - OG	-0.807	0.715	0.476	No
41-60 - 81-100	-4.547	4.571	< 0.001	Yes
41-60 - 100+	-0.720	0.853	0.395	No
41-60 - OG	-2.788	2.782	0.006	No
81-100 - 100+	3.827	3.616	< 0.001	Yes
81-100 - OG	1.759	1.481	0.141	No
100+ - OG	-2.068	1.941	0.055	No

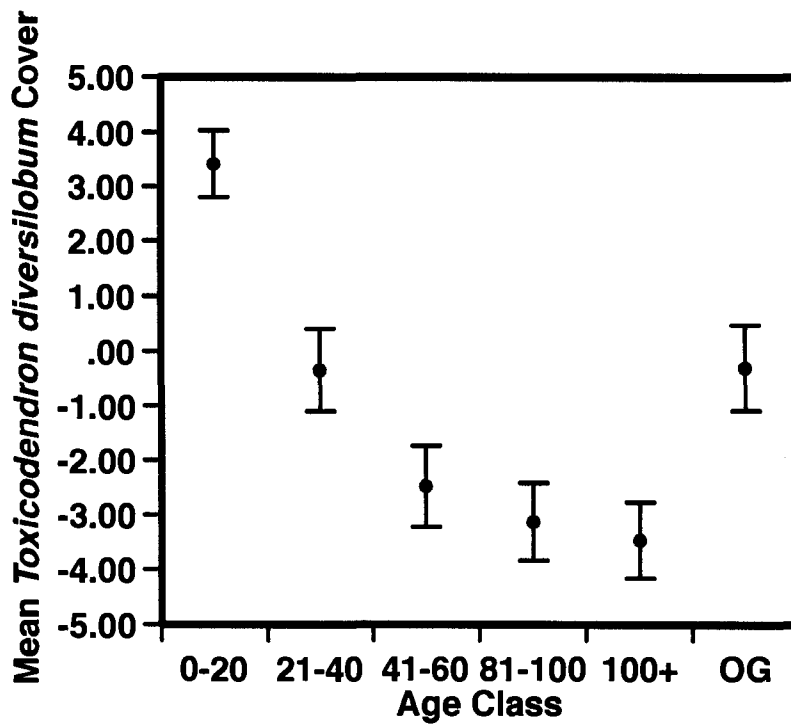


Figure 32. One-Way ANOVA between mean *Toxicodendron diversilobum* cover (m<sup>2</sup>/hectare) and age class in regenerating and old-growth forests.

Table 28. Mean *T. diversilobum* cover post hoc comparisons between age classes.

Bonferroni Test for Differences Between Means				
Adjusted $\alpha = 0.003$				
Groups	Difference	Statistic	P	Significant
0-20 - 21-40	3.751	3.863	< 0.001	Yes
0-20 - 41-60	5.879	6.133	< 0.001	Yes
0-20 - 81-100	6.523	7.002	< 0.001	Yes
0-20 - 100+	6.859	7.430	< 0.001	Yes
0-20 - OG	3.707	3.732	< 0.001	Yes
21-40 - 41-60	2.129	2.019	0.046	No
21-40 - 81-100	2.773	2.692	0.008	No
21-40 - 100+	3.108	3.041	0.003	Yes
21-40 - OG	-0.043	0.040	> 0.5	No
41-60 - 81-100	0.644	0.632	> 0.5	No
41-60 - 100+	0.980	0.970	0.334	No
41-60 - OG	-2.172	2.020	0.046	No
81-100 - 100+	0.336	0.341	> 0.5	No
81-100 - OG	-2.816	2.679	0.008	No
100+ - OG	-3.152	3.020	0.003	Yes

Approximately 40% of exotic species decreased significantly in cover as age after harvest increased. Specifically, the area occupied by *Hypochaeris glabra* (smooth cat's ear) ( $p=0.003$ ,  $r^2=0.029$ ), *Cortaderia selloana* (pampas grass) ( $p=0.004$ ,  $r^2=0.027$ ), *Arabidopsis thaliana* (moose ear cress) ( $p=0.006$ ,  $r^2=0.026$ ), *Leontodon taraxacoides* (white-flowered hawk bit) ( $p=0.024$ ,  $r^2=0.017$ ), and *Sonchus asper* (spiny sow thistle) ( $p=0.045$ ,  $r^2=0.013$ ) all decreased significantly as the age of the stand increased. All other exotic species decreased in cover with increasing stand age, but not significantly. There were no exotic species found in any stands older than 60 years or any of the old-growth stands sampled.

A few understory species that also occurred in more than 10% of plots sampled did not yield a significant difference between regenerating age classes, but were higher in old-growth stands compared to any other age class. *Vaccinium parvifolium* (huckleberry), *Galium triflorum* (sweet-scented bedstraw), and *Pteridium aquilinum* var. *pubescens* (bracken fern) exhibited the most cover in old-growth stands compared to regenerating stands. A number of native species only occurred in old-growth forests. These species included: *Anemone deltoidea* (windflower), *Rhamnus purshiana* (cascara buckthorn), *Euonymus occidentalis* (western burning bush), and *Rubus spectabilis* var. *franciscanus* (salmonberry).

## Discussion

This is the first study of its kind to analyze community level effects from harvesting in redwood forests, particularly within the redwood range of Mendocino County. Several significant relationships between regenerating redwood forests and community variables are apparent from the results of this study. These results concerning stand and understory dynamics have important implications for restoration and management for the north-central range of redwood forest communities.

### *Stand Dynamics*

Overall analyses of multiple variables showed a clear distinction between younger stands and older stands. The youngest stands (0-20 years) were characterized by much smaller diameter, denser tree populations. These sites supported more species of trees and canopy cover was patchy. Stands older than 80 years exhibited a higher dominance of trees, in particular redwoods, and stands were less dense. Older stands (100+ years) had fewer tree species and variable canopy cover. These results are supported by previous research, which characterized older stands as communities with fewer individual trees that dominated the stand causing low tree species richness (Busing & Fujimori, 2002, 2005; Fujimori, 1977). Additionally, total tree density, canopy cover, total basal area, specific species basal area, and specific species Importance Value significantly changed with stand age.

Total tree density decreased after clearcut harvest. At 41-60 years after timber harvest, tree densities began to approach those of old-growth stands. Fritz (1945) found

total tree density also decreased after harvest within a permanently established naturally-regenerating one-acre sample plot. However, the majority of previous research concluded that active management of regenerating stands is necessary in order for densities to approach old-growth levels (Lindquist, 2004a, 2004b; Oliver, et al.). In this study, total tree density showed a natural change towards old-growth levels of tree density without any active management, or thinning, of stands.

Canopy cover exhibited a pattern different from tree density, as percent canopy cover did not approach old-growth levels until stands were 81-100 years old. Old-growth forests had the most canopy cover, but remained isolated to patches, due to an increase in canopy complexity and insularity (Loya & Jules, 2007). Although younger stands were highest in tree density, the intermediate stages illustrated levels of canopy cover approaching old-growth status. This suggests that canopy cover, although highly variable, began to move toward old-growth levels in the middle stages of regeneration, which could allow for understory development to take place. Although canopy was much closer to the forest floor in intermediate aged stands, contrasting with the high canopy cover of older sites, intermediate stages of regeneration still allowed for similar levels of understory species development as old-growth forests. As with density, the cover of these naturally-regenerating stands approached that of old-growth stands without active management.

Total basal area significantly increased in regenerating stands, similar to canopy cover, after clearcut timber harvest, while tree density decreased. Old-growth forests

encompassed the highest combined basal area than any other age group. High basal area is characteristic of old-growth forests (Busing & Fujimori, 2002, 2005) and can be attributed to the dramatic growth of the dominant species, *Sequoia sempervirens* (Fritz, 1945). Basal area consistently increased throughout regenerating stands and were similar to old-growth stands within 81-100 years. Previously, basal area of tree species in redwood forests were managed to approach old-growth levels (Lindquist, 2004a, 2004b; Oliver, et al.). However, in these unmanaged stands sampled, basal area successfully resembled old-growth communities.

Community heterogeneity, including tree species richness, tree species diversity, and overall species richness, decreased with stand age. These indicators of species diversity were highest immediately after harvest, but declined in subsequent age groups, most likely due to the increased availability of resources immediately after harvest, such as greater soil fertility, solar radiation, and habitable landscapes (Tilman, 1985; Fraterrigo et al., 2006). At the intermediate 41-60 stage, tree species richness and the Shannon-Weiner Diversity Index of tree species began to resemble levels of old-growth stands. After an initial movement towards old-growth levels at 41-60 years after harvest, there was a subsequent increase in the 81-100 stage and a decrease in the 100+ stage. Richness and diversity of tree species decreased with stand age due to the increase in dominance of fewer species, especially redwood, in distinctive patches. Research by Busing and Fujimori (2002, 2005) also illustrated a high level of *S. sempervirens* dominance in old-growth forests, which resulted in a decrease of tree species richness and diversity in these



stands. Tree diversity was also low since most species in old-growth forests are adapted to tolerate the sun and nutrient deficiencies of this forest community (Hickman, 1993). Tree species richness and diversity were capable of approaching old-growth levels in naturally-regenerating redwood forests in intermediate stages of development.

Total species richness, including understory species, also decreased with age after clearcut harvest, but began to resemble old-growth forests at an earlier stand age than tree diversity and tree richness. As soon as 21-40 years after harvest, total understory species richness illustrated levels similar to old-growth stands. Old-growth communities exhibited a high level of patchiness consisting of fewer species. This pattern of development was also highly prevalent in old-growth stands in previous research (Busing & Fujimori, 2002). Overall species richness changed, moving towards levels found in old-growth stands, in an early intermediate stage (21-40) of development in these unmanaged redwood stands.

Several specific tree species showed a significant change following clearcut harvest within the Big River Watershed. *Sequoia sempervirens* increased in basal area and Importance Value after clearcut harvest and had the greatest increase in basal area with stand age of any tree species. Basal area of *S. sempervirens* consistently increased in regenerating stands but did not resemble areas typical of old-growth stands until after at least 100 years since harvest. As has been found in previous research, redwood trees in old-growth stands had the highest basal area (Busing & Fujimori, 2002, 2005; Fujimori, 1977; Russell & Jones, 2001). Although redwood basal area also increased over time

following selective cut harvest in previous work (Cole, 1983; Lindquist, 2004a, 2004b; Oliver et al., 1994), this study suggests that additional time may be necessary to fully resemble old-growth levels in naturally-regenerating redwood communities. However, *Sequoia sempervirens* had the greatest increase in overall Importance Value with stand age and was similar to old-growth importance much sooner, in the 41-60 age class. These results indicate that Importance Value of redwood will resemble old-growth forests in an early intermediate stage followed by an increase in basal area in a natural setting.

Due to the regenerative capability of *Sequoia sempervirens*, the complexity of the disturbance regime in redwood communities also increased over time. Disturbances became highly stochastic and unpredictable as stands aged. Single-tree windfalls were the main impetus for community change in mature regenerating stands and in old-growth forests, resulting in small gaps in the forest canopy, consistent with previous research (Sawyer, Sillett, Popenoe, et al., 2000). Restoration involving the active removal of canopy species within these redwood communities may alter the disturbance regime and the development of native plant communities.

Similar to *Sequoia sempervirens*, *Tsuga heterophylla* (western hemlock) also increased in basal area and Importance Value with stand age, peaking within the 41-60 range after harvest for both parameters. Following redwood, *T. heterophylla* was the most important tree species sampled and was highly prevalent in old-growth stands, indicating that hemlock is a critical associate species in redwood-dominated old-growth forests. As a shade-tolerant species (Hickman, 1993), *T. heterophylla* was able to survive

throughout the development of the unmanaged redwood stands sampled. Although hemlock basal area and Importance Value within the 100+ age class were closest to levels in old-growth stands, change reflecting old-growth levels occurred in the 41-60 age group.

Other tree species parameters decreased approaching old-growth aged stands, including *Pseudotsuga menziesii* var. *menziesii* (Douglas-fir) basal area, *Lithocarpus densiflorus* (tanoak) basal area and Importance Value, *Umbellularia californica* (California bay) Importance Value, and *Abies grandis* (grand fir) Importance Value. As the dominance and importance of *S. sempervirens* increased, the dominance and importance of other species decreased, which mirrored conditions in old-growth stands. However, both tanoak and Douglas-fir were common co-dominant species throughout the development of these stands, supported by previous research (Zinke, 1988). The development of other tree species in regenerating stands, which eventually approached old-growth levels in each case, suggests that movement towards old-growth levels may occur in a naturally-regenerating redwood forest without additional management.

There is no previous research that discusses the change in basal area or Importance Value following clearcut harvest in regenerating redwood communities. Total dominance of all tree species significantly increased over time and exhibited very high levels in old-growth sites. *Sequoia sempervirens* and *Tsuga heterophylla* increased in basal area and importance over time after clearcut harvest and were also highest in the old-growth stands sampled. These results suggest, if given adequate time to regenerate,

total basal area, basal area of specific species, and Importance Value of individual tree species were capable of returning to old-growth levels without the involvement of active management.

### *Understory Dynamics*

In addition to stand parameters, several understory parameters, including overall cover, herb cover, understory diversity, understory richness, and understory evenness illustrated community change towards old-growth stands. The cover of exotic species decreased, while cover of native species increased with stand age following harvest. The development of the understory in these regenerating redwood forests has previously not been studied and will also require additional research.

Cover of native understory species illustrated a bimodal distribution after clearcut harvest. Total understory cover initially decreased immediately after harvest, reaching the lowest cover within 41-60 years. After this initial decline, cover of native understory species began to increase significantly. Due to the bimodal pattern of development, cover of understory species was closest to old-growth levels immediately after harvest, but a subsequent increase in total cover occurred in the 81-100 age group. The cover of herbaceous species also illustrated a similar pattern in the regenerating stands, suggesting the ability of understory species to recover after harvest in these unmanaged forests, provided sufficient time. Loya and Jules (2007) also found understory cover was highest in early stages of development following clearcut harvest.

The cover of native understory species was higher in old-growth stands than any other age of regenerating forest. Although Loya and Jules (2007) concluded overall cover was lowest in old-growth stands, Rivas-Ederer and Kjeldsen (1998) found that old-growth stands exhibited the highest amount of understory cover. However, Rivas-Ederer and Kjeldsen did not evaluate development of naturally-regenerating redwood forests, since herbicide application and planting took place after harvest. This thesis study found that herbaceous cover had an almost identical pattern of development as total understory cover, but visibly approached old-growth levels within 41-60 years in regenerating stands. Although old-growth stands were mostly located in visited tourist areas, one old-growth site sampled in this study, located within the Russell redwood property, is the least disturbed remaining old-growth stand on the Mendocino coast and is the most representative of old-growth communities of this region. These findings reveal that cover of understory species was capable of approaching old-growth levels without post-harvest management within the stands sampled of the Big River Watershed.

Diversity indicators of native understory species, including richness, evenness, and the Shannon-Weiner Diversity Index, also approached old-growth status after clearcut timber harvest. Species richness decreased with stand age and illustrated lower levels in old-growth forests. Species richness was also low in old-growth forests in previous research (Loya & Jules, 2007). Regenerating stands began to approach this level of richness in the 81-100 year range. Species evenness and the Shannon-Weiner Diversity Index of understory species both increased after harvest, peaked in the 41-60

age group, but then decreased to resemble old-growth forests. The youngest age group closely resembled old-growth forests, due to the bimodal convex shape of understory development. Subsequently, understory evenness and diversity levels began to move towards old-growth levels within the 100+ age group. Old-growth stands had the lowest levels of understory species evenness and diversity, mainly due to an increase in dominance of fewer species tolerant of this specialized environment (Loya & Jules). Overall richness, evenness, and diversity of understory species were capable of recovery in regenerating stands without active management.

Cover of specific understory species illustrated a significant change after harvest, resembling old-growth forests in older stands. Herbaceous species native to California, including *Trillium ovatum* (Pacific trillium), *Tiarella trifoliata* var. *unifoliata* (sugar scoop), *Oxalis oregana* (redwood sorrel), and *Viola sempervirens* (redwood violet) significantly increased after harvest. Native shrub species, *Gaultheria shallon* (salal), *Rhododendron macrophyllum* (California rhododendron), and *Toxicodendron diversilobum* (poison oak), also illustrated a significant movement within age groups and compared to old-growth stands. This is the first study to analyze the development of a suite of understory species after clearcut harvest within several regenerating and old-growth redwood communities.

The cover of a majority of herbaceous species increased in regenerating stands and exhibited high levels of cover in old-growth stands. *T. ovatum*, *T. trifoliata* var. *unifoliata*, and *O. oregana* followed this pattern of development, indicating the ability of

these common redwood species to eventually recover in naturally-regenerating redwood forests. *T. ovatum* began to resemble old-growth forests in the 81-100 age group. Although *T. ovatum* is almost completely destroyed after clearcut harvest (Jules, 1998), this study illustrated that Pacific trillium was capable of natural recovery in these regenerating stands sampled. *T. trifoliata* var. *unifoliata*, *O. oregana*, *V. sempervirens* approached old-growth levels within the 100+ range, slightly later than *T. ovatum*. Each species illustrated an ability to move towards old-growth levels in the unmanaged stands of the Big River Watershed.

Shrub species *Gaultheria shallon* (salal), *Rhododendron macrophyllum* (California rhododendron), and *Toxicodendron diversilobum* (poison oak), varied in regenerating stands but were prevalent in old-growth stands. *G. shallon* resembled old-growth stands at 81-100 years after harvest, while *R. macrophyllum* and *T. diversilobum* visibly began to approach old-growth levels within the 100+ stage. *R. macrophyllum* and *T. diversilobum* had a slight bimodal concave distribution, which could indicate these species may take longer to advance towards old-growth levels. However, all of these species grow throughout the redwood range (Lyons & Cuneo-Lazaneo, 2003), and illustrated an ability to recover without active management.

Exotic species were present in early age groups following harvest, but cover declined with stand age. Exotics were completely absent from stands 60 years or older, including the old-growth forests. Greatest declines were exhibited by *Hypochaeris glabra* (smooth cat's ear), *Cortaderia selloana* (pampas grass), *Arabidopsis thaliana*

(moose ear cress), *Leontodon taraxacoides* (white-flowered hawk bit), and *Sonchus asper* (spiny sow thistle). Loya & Jules (2007) also found few exotic species in old-growth stands. The introduction of exotic species has increased in California over the last century (Raven, 1988) and it might be that older stands of regenerating redwoods simply were not as exposed to non-natives as the younger stands. However, the most dominant exotic species found within the Big River Watershed, *Cortaderia selloana* (pampas grass), was first introduced into California in 1848 (Lambrinos, 2001), before the initial harvest of the oldest stands sampled in this study. These results suggest that pampas grass, and perhaps other exotic species, may establish in young regenerating stands but over time give way to native species and eventually completely disappear in unmanaged, naturally-regenerating redwood forest communities.

Immediately after clearcut harvest, sites fluctuated in canopy gap size, producing a wide range of conditions. Previous land use that could not be determined included condition of sites when logging operations ceased, the length of time it took crews to excavate, the procedures taken by crews while excavating, and whether or not salvage logging took place. Other variables, such as slope, aspect, and edaphic parameters, also varied to a degree between sites. Use of a post hoc chronosequence analysis helped limit the amount of variation between sites, allowing this study to provide preliminary data on the redwood forest communities of the Big River Watershed.

This study explicitly addresses the development of stand parameters, specific tree species, understory parameters, and specific understory species in naturally-regenerating



redwood forests of the Big River Watershed. The results indicate that the dominance of native species increased with stand age following harvest, while exotic species were absent in older stands and old-growth stands. There is little previous research regarding the development following clearcut harvest in unmanaged regenerating redwood forests, and additional research is necessary to further demonstrate the development of these communities. As the most comprehensive study of its kind to date, this research provides a baseline for restoration recommendations and future research.

## Recommendations

The results of this study illustrate that community parameters and individual species were capable of natural recovery without active management in the regenerating redwood communities sampled of the Big River Watershed in Mendocino County, California. Management of these communities that results in the removal of canopy species, including thinning, may negatively impact the development of these stands. Recommendations from this study may lead to community recovery and increase the continuity of the remaining redwood forests.

*Sequoia sempervirens* are distinctive tree species as a result of their unique regenerative capabilities, high resilience to disturbances, and high tolerance levels. Redwood forest communities are endemic to the Pacific coast and differ from other forest types due to the unpredictable regeneration patterns of *Sequoia sempervirens* and the rapid increase in dominance of this species following timber harvest. Specialized native plant species are also adapted to the distinct conditions in these forests. In regenerating redwood forests, natural management practices could allow for restoration without additional human disturbance, which may impede community recovery. Findings from this study indicate regenerating redwood forest communities and specific species were capable of recovery without the active manipulation of traditional management practices.

Regenerating redwood stands within the Big River Watershed did not require any active management in order to regain old-growth features. Older sites were relatively undisturbed, even from trail use or recreation activities, and existed in fairly remote,

preserved areas distant from local populations. These sites have the potential to eventually resemble old-growth forests and retain developing old-growth characteristics if allowed to regenerate naturally. A summary of concluding results illustrates findings for restoration (Appendix C). Overall, the continuation of a natural management policy may allow these communities to recover without additional disturbance.

General recommendations for restoration in these regenerating redwood forests includes a natural approach to management. The sites sampled were highly fragmented due to various harvest age and recent land use. If sites continue to be undisturbed, there may be an increase in the overall continuity of the regenerating redwood forest communities within this region. Due to the sensitivity of these areas, any removal of foreign material should take place on a small scale with extreme caution. Most of the unused remnant logging roads supported native plant communities, which could be left to regenerate naturally. However, prominent logging roads caused an unnatural sharp contrast in elevation and did not allow for species establishment. Continued presence or use of these roads could increase erosion, impact edaphic health, and damage adjacent aquatic habitats. Major roads should be decommissioned and restored to a natural setting to mitigate the effects from past land use.

Exotic species did not appear in stands 60 years or older following clearcut timber harvest and were completely absent in old-growth stands. Exotic species may have been out-competed in the older stands or these non-native species may not have occurred until the older cuts were well advanced in succession. Whether non-natives establish in newly

cut stands or are pushed out by natives over time requires further study. The introduction of exotic species into California has increased since the older stands in this study were initially harvested, which may have contributed to the absence of exotic species in these sites. However, exotics were found at the periphery of older stands and old-growth stands, but not within these sites. Additional research on exotic species in regenerating redwood forests will clarify the regenerative nature of these species.

Although the results from this study indicate regenerating redwood forests of the Big River Watershed were capable of natural recovery, limitations of this study could be clarified through additional research. This study focused on the vegetative change in redwood forests following harvest in a chronosequence, although several other factors beyond the scope of this study contributed to the development of these forest communities. Future research monitoring the stands sampled in this study could include the impact on soil relations, fungal associations, or fauna biodiversity. A comparison of community developmental patterns in redwood forests following different harvest methods, such as selective harvest, could also add to this study in determining the effects of timber harvest. The regenerating redwood forests of Mendocino county are the least studied, and should continue as a focal point for forest ecologists.

Currently under the jurisdiction of California State Parks, the Russell redwood property has the potential to become a permanent research station in Mendocino County. Located amidst relatively undisturbed and naturally-regenerating second-growth and old-growth redwood forests, this area is the most representative of plant communities and

development in the region. Facilities are already in place on the Russell redwood property and offer a rare opportunity to study the few remaining naturally developing redwood forests and old-growth redwood forests of the north-central coast range.

A detailed understanding of community development is necessary to manage recovering redwood forests. The current management paradigm focuses on specific tree species and does not assess impacts on community heterogeneity. Timber harvest effects on the entire redwood community may damage recovering stands, which should be taken into account in developing restoration efforts. The remaining redwood forests are largely fragmented, increasing the importance of restoring the overall continuity of the redwood range. If allowed sufficient time to develop after harvest incorporating a natural management approach, existing regenerating coast redwood communities within the Big River Watershed will increasingly resemble old-growth redwood stands and effectively restore these remarkable habitats.

## References

- Barbour, M., Lydon, S., Borchert, M., Popper, M., Whitworth, V., & Evarts, J. (2001). *Coast redwood: A natural and cultural history*. Los Olivos, CA: Cachuma Press.
- Becking, R. (1982). *Pocket flora of the redwood forest*. Covelo, CA: Island Press.
- Benda, L.E., Bigelow, P., & Worsley, T.M. (2002). Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, U.S.A. *Canadian Journal of Forest Research*, 32, 1460-1477.
- Boe, K. (1965). *Natural regeneration in old-growth redwood cuttings*. (USFWS Research Note PSW 94). Berkeley, CA: Pacific Southwest Forest and Range Experiment Station.
- Bosch, C.A. (1971). Redwoods: A population model. *Science*, 172(3981), 345-349.
- Brumelis, G. & Carleton, T.J. (1989). The vegetation of post-logged black spruce lowlands in central Canada. *Journal of Applied Ecology*, 26, 321-339.
- Brussard, P.F., Levin, S.A., Miller, L.N., Whittaker, R.H., Halbach, K., Diem, J.E., et al. (1971). Redwoods: A Population Model Debunked. *Science*, 174(4007), 435-436.
- Burgess, S.S.O. & Dawson, T.E. (2004). The contribution of fog to the water relations of *Sequoia sempervirens* (D.Don): foliar uptake and prevention of dehydration. *Plant, Cell and Environment*, 27, 1023-1034.
- Busing, R.T. & Fujimori, T. (2002). Dynamics of composition and structure in an old *Sequoia sempervirens* forest. *Vegetation Science*, 13, 785-792.
- Busing, R.T. & Fujimori, T. (2005). Biomass, production and woody detritus in an old coast redwood (*Sequoia sempervirens*) forest. *Plant Ecology*, 177, 177-188.
- Cain, S. (1938). The Species-Area Curve. *American Midland Naturalist*, 19(3), 573-581.
- California Department of Parks and Recreation. (2006). *Draft Initial Study/Mitigated Negative Declaration*. Big River Watershed Restoration, Mendocino Headlands State Park. Mendocino, CA.

- Carey, A. (2006). Active and passive forest management for multiple values. *Northwestern Naturalist*, 87, 18-30.
- Cattelino, P.J., Noble, I.R., Slatyer, R.O., & Kessell, S.R. (1979). Predicting multiple pathways of plant succession. *Environmental Management*, 3(1), 41-50.
- Clements, F.E. (1916). *Plant succession: an analysis of the development of vegetation*. Washington, D.C.: Carnegie Institution of Washington.
- Clements, F.E. (1928). *Plant succession and indicators*. New York, NY: H.W. Wilson Publishing.
- Clements, F.E. (1936). Nature and structure of the climax. *Journal of Ecology*, 24(1), 252-284.
- Clements, F.E., Hanson, H.C., & Weaver, J.E. (1929). *Plant competition: an analysis of community functions*. Washington, D.C.: Carnegie Institution of Washington.
- Cole, D.W. (1983). Redwood sprout growth three decades after thinning. *Journal of Forestry*, 81, 148-157.
- Compton, R.C. (1985). Percentage diagrams for estimating composition by volume. In *Geology in the field* (pp. 366-367). New York, NY: John Wiley & Sons.
- Connell, J.H. & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, 111(982), 1119-1144.
- Conrad, J.M. (1997). On the option value of old-growth forest. *Ecological Economics*, 22, 97-102.
- Corns, I.W. (1988). Compaction by forestry equipment and effects on coniferous seedling growth on four soils in the Alberta foothills. *Canadian Journal of Forest Research*, 18, 75-84.
- Costa, F. & Magnusson, W. (2002). Selective logging effects on abundance, diversity, and composition of tropical understory herbs. *Ecological Applications*, 12(3), 807-819.

- Curtis, J.T. & McIntosh, R.P. (1951). An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, 32(3), 476-496.
- DeClerck, F.A., Barbour, M.G., & Sawyer, J.O. (2005). Resource use efficiency as a function of species richness and stand composition in upper montane conifer forests of the Sierra Nevada. *Journal of Vegetation Science*, 16, 443-452.
- DeJong, T.M. (1975). A comparison of three diversity indices based on their components of richness and evenness. *Oikos*, 26(2), 222-227.
- Dignan, P. & Bren, L. (2003). A study of the effect of logging on the understorey light environment in riparian buffer strips in a south-east Australian forest. *Forest Ecology and Management*, 172, 161-172.
- Douhovnikoff, V., Cheng, A.M., & Dodd, R.S. (2004). Incidence, size, and spatial structure of clones in second-growth stands of Coast Redwood, *Sequoia sempervirens* (Cupressaceae). *American Journal of Botany*, 91(7), 1140-1146.
- Duffy, C.D. & Meier, A.J. (1992). Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology*, 6(2), 196-201.
- Dyrness, C.T. (1973). Early stages of plant succession following logging and burning in Western Cascades of Oregon. *Ecology*, 54(1), 57-69.
- Ebrecht, L. & Schmidt, W. (2003). Nitrogen mineralization and vegetation along skidding tracks. *Annals of Forest Science*, 60, 733-740.
- Fraterrigo, J.M., Turner, M.G., & Pearson, S.M. (2006). Interactions between past land use, life-history traits and understorey spatial heterogeneity. *Landscape Ecology*, 21, 777-790.
- Fritz, E. (1930, October). *The role of fire in the redwood region*. Paper presented at the meeting of the California Section of the Society of American Foresters, San Francisco, CA.
- Fritz, E. (1945). Twenty years' growth on a redwood sample plot. *Journal of Forestry*, 43, 30-36.



- Fritz, E. (1950, December). *Some principles governing the growing of redwood crops*. Paper presented at the meeting of the Western Forestry and Conservation Association, San Francisco, CA.
- Fritz, E. (1957). The life and habits of redwood the extraordinary are described by an authority. *Western Conservation Journal*, 14(38), 4-7.
- Fujimori, T. (1977). Stem biomass and structure of a mature *Sequoia sempervirens* stand on the Pacific Coast of northern California. *Journal of Japanese Forest Society*, 59, 435-441.
- Gigawiz Ltd Co. (2007). Aabel 20/20 Data Vision. Software and User Guide. Version 2.4.
- Gilliam, F.S. (2002). Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA. *Forest Ecology and Management*, 155, 33-43.
- Gilliam, F.S. & Turrill, N.L. (1993). Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. *Bulletin of the Torrey Botanical Club*, 120(4), 445-450.
- Gilliam, F.S., Turrill, N.L., & Adams, M.B. (1995). Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications*, 5(4), 947-955.
- Gleason, H.A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53(1), 7-26.
- Gleason, H.A. (1927). Further views on the succession-concept. *Ecology*, 8(3), 299-326.
- Halpern, C.B. & Spies, T.A. (1995). Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications*, 5(4), 913-934.
- Hickman, J.C. (Ed.). (1993). *The jepson manual: Higher plants of California*. Berkeley, CA: University of California Press.
- Holl, K.D. (2002). Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *The Journal of Applied Ecology*, 39(6), 960-970.

- Hunter, J.C. & Parker, V.T. (1993). The disturbance regime of an old-growth forest in coastal California. *Journal of Vegetation Science*, 4, 19-24.
- Husinga, K.D., Laughlin, D.C., Fulé, P.Z., Springer, J.D., & McGlone, C.M. (2005). Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. *Journal of the Torrey Botanical Society*, 132(4), 590-601.
- Huston, M. (1979). A general hypothesis of species diversity. *The American Naturalist*, 113(1), 81-101.
- Jenkins, M.A. & Parker, G.R. (2001). Woody species composition of disturbed forests in intermittent stream bottomlands of southern Indiana. *Journal of the Torrey Botanical Society*, 128(2), 165-175.
- Jules, E.S. (1998). Habitat fragmentation and demographic change for a common plant: trillium in old-growth forest. *Ecology*, 75(5), 1645-1656.
- Jules, E.S. & Rathcke, B.J. (1999). Mechanisms of reduced trillium recruitment along edges of old-growth forest fragments. *Conservation Biology*, 13(4), 784-793.
- Jussy, J.H., Ranger, J., Bienaime, S., & Dambrine, E. (2004). Effects of a clear-cut on the in situ nitrogen mineralisation and the nitrogen cycle in a 67-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantation. *Annals of Forest Science*, 61(5), 397.
- Karadzic, B. & Popovic, R. (1994). A generalized standardization procedure in ecological ordination: tests with principal components analysis. *Journal of Vegetation Science*, 5, 259-262.
- Keane, R.E., Cary, G.J., Davies, I.D., Flannigan, M.D., Gardner, R.H., Lavorel, S., et al. (2004). A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. *Ecological Modeling*, 179, 3-27.
- Kenkel, N.C. & Podani, J. (1991). Plot size and estimation efficiency in plant community studies. *Journal of Vegetation Science*, 2(4), 539-544.
- Kimmins, J.P. (1987). *Forest ecology*. New York, NY: Macmillan Publishing.
- Koch, G.W., Sillett, S.C., Jennings, G.M., & Davis, S.D. (2004). The limits to tree height. *Nature*, 428, 851-854.

- Lambrinos, J.G. (2001). The expansion history of a sexual and asexual species of *Cortaderia* in California, USA. *Ecology*, 89(1), 88-98.
- Leigh Jr., E.G., Davidar, P., Dick, C.W., Puyravaud, J.P., Terborgh, J., Steege, H., et al. (2004). Why do some tropical forests have so many trees? *Biotropica*, 36(4), 447-473.
- Lindquist, J.L. (2004a). *Precommercial stocking control of coast redwood: A seventeen year status report (1981-1998)*. (California Forestry Report 2, 25 pp). Sacramento, CA: California Department of Forestry and Fire Protection.
- Lindquist, J.L. (2004b). *Growth and yield report for the whiskey springs redwood commercial thinning study: A twenty-nine year status report (1970-1999)*. (California Forestry Report 3, 25 pp). Sacramento, CA: California Department of Forestry and Fire Protection.
- Loya, D.T. & Jules, E.S. (2007). Use of species richness estimators improves evaluation of understory plant response to logging: a study of redwood forests. *Plant Ecology*, 194(2), 179-194.
- Lyons, K. & Cuneo-Lazaneo, M.B. (2003). *Plants of the coast redwood region*. Soquel, CA: Shoreline Press.
- Mahoney, T.M. & Stuart, J.D. (2004). *Status of vegetation classification in redwood ecosystems*. (USDA Forest Service Rep PSW-GTR-194). Vallejo, CA: United States Forest Service.
- McBride, J.R. (1977). *The ecology of redwood [*Sequoia sempervirens* (D. Don) Endl.] and the impact of man's use of the redwood forest as a site for recreational activities*. (United States National Park Service Report, 39 pp). Berkeley, CA: California Department of Forestry and Fire Protection.
- McCarthy, B.C., Hammer, C.A., Kauffman, G.L., & Cantino, P.D. (1987). Vegetation patterns and structure of an old-growth forest in southeastern Ohio. *Bulletin of the Torrey Botanical Society*, 114(1), 33-45.
- Noss, R.F. (2000). More than big trees. In R.F. Noss (Ed.), *The redwood forest: History, ecology, and conservation of the coast redwoods* (pp. 1-6). Washington D.C.: Island Press.

- Oliver, W.W., Lindquist, J.L., & Strothmann, R.O. (1994). Young-growth redwood stands respond well to various thinning intensities. *Western Journal of Applied Forestry*, 9(4), 106-112.
- Powers, R.F. & Wiant Jr., H.V. (1970). Sprouting of old-growth coastal redwood stumps on slopes. *Forest Science*, 16(3), 339-341.
- Raven, P.H. (1988). The California flora. In M.G. Barbour & J. Major (Eds.), *Terrestrial vegetation of California* (2nd ed, pp.109 -137). Sacramento, CA: California Plant Society Press.
- Rivas-Ederer, D. & Kjeldsen, C.K. (1998). *Seral vascular plant communities on clearcut sites in Jackson Demonstration State Forest, Mendocino County, California*. Sonoma State University, California Department of Forestry and Fire Protection. Rohnert Park, CA.
- Roberts, M.R. & Gilliam, F.S. (1995). Disturbance effects on herbaceous layer vegetation and soil nutrients in *Populus* forests of northern lower Michigan. *Journal of Vegetation Science*, 6(6), 903-912.
- Roy, D.F. (1966). *Silvicultural characteristics of redwood (Sequoia sempervirens [D.Don] Endl.)*. (USFS PSWF& RES Res. Paper PSW-28, 20 pp). Vallejo, CA: United States Forest Service.
- Russell, W.H. & Jones, C. (2001). The effects of timber harvesting on the structure and composition of adjacent old-growth coast redwood forest, California, USA. *Landscape Ecology*, 16, 731-741.
- Rutland, R. (2002). *Big River Land Use History 1852-2001*. Santa Rosa, CA: California Department of Forestry and Fire Protection.
- Sawyer, J.O., Sillett, S.C., Popenoe, J.H., LaBanca, A., Sholars, T., Largent, D.L., et al. (2000). Characteristics of redwood forests. In R.F. Noss (Ed.), *The redwood forest: History, ecology, and conservation of the coast redwoods* (pp. 39-79). Washington D.C.: Island Press.
- Sawyer, J.O., Sillett, S.C., Libby, W.J., Dawson, T.E., Popenoe, J.C., Largent, D.L., et al. (2000). Redwood trees, communities, and ecosystems: a closer look. In R.F. Noss (Ed.), *The redwood forest: History, ecology, and conservation of the coast redwoods* (pp. 81-118). Washington D.C.: Island Press.

- Scheller, R.M. & Mladenoff, D.J. (2002). Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecological Applications*, 12(5), 1329-1343.
- Shugart, H.H., Jr. & West, D.C. (1980). Forest succession models. *BioScience*, 30(5), 308-313.
- Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology and Evolution*, 19(11), 605-610.
- Skeen, J.N. (1973). An extension of the concept of importance value in analyzing forest communities. *Ecology*, 54(3), 655-656.
- Smith, G. & Wheeler, C.R. (1992). *A flora of the vascular plants of Mendocino County, California*. San Francisco: University of San Francisco.
- Stephens, S.L. & Fry, D.L. (2005). Fire history in coast redwood stands in the northeastern Santa Cruz mountains, California. *Fire Ecology*, 1(1), 2-19.
- Stone, M.K. & Wallace, J.B. (1998). Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. *Freshwater Biology*, 39, 151-169.
- Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *The American Naturalist*, 125(6), 827-852.
- United States Fish and Wildlife Service. (1997). *Recovery plan for the marbled murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California*. Portland, OR: United States Fish and Wildlife Service.
- Veirs, S.D., Jr. (1996, June). Ecology of the coast redwood. In *Proceedings of the Conference on Coast Redwood Forest Ecology and Management*. Symposium conducted at Humboldt State University, Arcata, California.
- Waring, R.H. & Major, J. (1964). Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light and temperature. *Ecological Monographs*, 34(2), 167-215.
- Watt, A.S. (1947). Pattern and process in the plant community. *The Journal of Ecology*, 35(12), 1-22.

- Watts, P. (2002). *Redwood region flower finder: A guide to identifying wildflowers of the coastal fog belt of California* (2nd ed.). Rochester, NY: Nature Study Guild.
- Wensel, L.C., Daugherty, P.J., & Meerschaert, W.J. (1986). CACTOS user's guide: Agricultural Experiment Station, University of California, Berkeley, Division of Agriculture and Natural Resources, Bulletin 1920.
- Wensel, L.C., Krumland, B., & Meerschaert, W.J. (1982). CRYPTOS user's guide: Agricultural Experiment Station, University of California, Berkeley, Division of Agriculture and Natural Resources, Bulletin 1924.
- Whitmore, S. (1989). Canopy gaps and the two major groups of forest trees. *Ecology*, 70, 536-538.
- Whittaker, R.H. (1953). A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs*, 23(1), 41-78.
- Whittaker, R.J., Willis, K.J., & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28(4), 453-470.
- Yorks, T.E., Dabydeen, S., & Smallidge, P.J. (2000). Understory vegetation-environment relationships in clearcut and mature secondary forests of western Maryland. *Northeastern Naturalist*, 7(3), 205-220.
- Zinke, P.J. (1988). The redwood forest and associated north coast forests. In M.G. Barbour & J. Major (Eds.), *Terrestrial vegetation of California* (2nd ed., pp. 670-699). Sacramento, CA: California Plant Society Press.

Appendix A. Non-response variable data and dominant canopy species

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
0-20	1	28	45	UMCA	32.94
0-20	2	33	50	LIDE	32.94
0-20	3	24	325	PSME	32.94
0-20	4	38	350	ABGR	32.94
0-20	5	9	28	UMCA	32.94
0-20	6	42	99	ABGR	32.94
0-20	7	29	44	PSME	32.94
0-20	8	38	356	LIDE	32.94
0-20	9	44	342	PSME	32.94
0-20	10	41	310	LIDE	32.94
0-20	11	28	306	PSME	32.94
0-20	12	34	352	LIDE	32.94
0-20	13	35	344	LIDE	32.94
0-20	14	24	289	SESE	32.94
0-20	15	33	268	SESE	32.94
0-20	16	31	323	SESE	32.94
0-20	17	30	29	LIDE	32.94
0-20	18	34	13	ALRU	32.94
0-20	19	34	320	TSHE	32.94
0-20	20	28	319	LIDE	32.94
0-20	21	28	60	LIDE	12.62
0-20	22	45	73	LIDE	12.62
0-20	23	38	41	LIDE	12.62
0-20	24	45	100	LIDE	12.62
0-20	25	22	77	LIDE	12.62
0-20	26	32	83	LIDE	12.62
0-20	27	38	119	SESE	12.62
0-20	28	25	64	LIDE	12.62
0-20	29	22	97	LIDE	12.62
0-20	30	24	169	LIDE	12.62
0-20	31	50	205	UMCA	12.62
0-20	32	48	165	SESE	12.62
0-20	33	45	174	SESE	12.62
0-20	34	26	186	SESE	12.62
0-20	35	55	122	UMCA	12.62
0-20	36	39	121	SESE	12.62
0-20	37	43	144	LIDE	12.62
0-20	38	31	52	LIDE	12.62
0-20	39	22	215	LIDE	12.62

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
0-20	40	23	46	LIDE	12.62
0-20	41	33	13	UMCA	17.37
0-20	42	34	323	SESE	17.37
0-20	43	34	180	LIDE	17.37
0-20	44	46	180	UMCA	17.37
0-20	45	34	304	SESE	17.37
0-20	46	25	50	PSME	17.37
0-20	47	32	334	PSME	17.37
0-20	48	43	324	PSME	17.37
0-20	49	24	43	LIDE	17.37
0-20	50	29	3	LIDE	17.37
0-20	51	33	347	PSME	17.37
0-20	52	32	329	SESE	17.37
0-20	53	42	354	PSME	17.37
0-20	54	52	170	UMCA	17.37
0-20	55	32	25	UMCA	17.37
0-20	56	34	332	PSME	17.37
0-20	57	34	35	PSME	17.37
0-20	58	25	14	PSME	17.37
0-20	59	38	44	SESE	17.37
0-20	60	48	10	PSME	17.37
21-40	61	35	353	SESE	11.63
21-40	62	40	58	LIDE	11.63
21-40	63	42	356	SESE	11.63
21-40	64	26	12	LIDE	11.63
21-40	65	47	53	UMCA	11.63
21-40	66	17	119	LIDE	11.63
21-40	67	23	262	SESE	11.63
21-40	68	34	92	SESE	11.63
21-40	69	41	68	SESE	11.63
21-40	70	28	250	SESE	11.63
21-40	71	39	270	LIDE	11.63
21-40	72	26	142	SESE	11.63
21-40	73	23	106	LIDE	11.63
21-40	74	38	26	LIDE	11.63
21-40	75	48	129	UMCA	11.63
21-40	76	38	123	PSME	11.63
21-40	77	42	104	SESE	11.63
21-40	78	49	87	LIDE	11.63



<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
21-40	79	39	56	PSME	11.63
21-40	80	48	132	PSME	11.63
21-40	81	26	28	SESE	3.23
21-40	82	46	81	LIDE	3.23
21-40	83	43	54	SESE	3.23
21-40	84	39	24	LIDE	3.23
21-40	85	12	112	LIDE	3.23
21-40	86	28	83	LIDE	3.23
21-40	87	42	121	LIDE	3.23
21-40	88	34	66	SESE	3.23
21-40	89	32	26	LIDE	3.23
21-40	90	47	342	LIDE	3.23
21-40	91	20	97	LIDE	3.23
21-40	92	29	76	LIDE	3.23
21-40	93	34	15	ALRU	3.23
21-40	94	30	63	LIDE	3.23
21-40	95	36	92	SESE	3.23
21-40	96	23	14	LIDE	3.23
21-40	97	32	300	LIDE	3.23
21-40	98	38	266	SESE	3.23
21-40	99	32	75	LIDE	3.23
21-40	100	21	50	LIDE	3.23
21-40	101	13	72	SESE	4.22
21-40	102	9	77	LIDE	4.22
21-40	103	33	42	LIDE	4.22
21-40	104	19	64	LIDE	4.22
21-40	105	23	103	LIDE	4.22
21-40	106	32	85	LIDE	4.22
21-40	107	38	84	LIDE	4.22
21-40	108	17	68	LIDE	4.22
21-40	109	19	94	LIDE	4.22
21-40	110	32	68	LIDE	4.22
21-40	111	12	90	SESE	4.22
21-40	112	24	117	SESE	4.22
21-40	113	18	86	LIDE	4.22
21-40	114	15	119	LIDE	4.22
21-40	115	17	38	PSME	4.22
21-40	116	7	64	LIDE	4.22
21-40	117	33	89	LIDE	4.22

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
21-40	118	6	52	SESE	4.22
21-40	119	23	55	LIDE	4.22
21-40	120	21	103	SESE	4.22
41-60	121	24	212	SESE	9.72
41-60	122	26	141	SESE	9.72
41-60	123	19	180	SESE	9.72
41-60	124	28	181	PSME	9.72
41-60	125	40	197	SESE	9.72
41-60	126	26	178	SESE	9.72
41-60	127	13	145	PSME	9.72
41-60	128	14	108	SESE	9.72
41-60	129	8	230	SESE	9.72
41-60	130	28	245	SESE	9.72
41-60	131	30	205	SESE	9.72
41-60	132	12	199	SESE	9.72
41-60	133	38	187	SESE	9.72
41-60	134	25	220	SESE	9.72
41-60	135	26	232	SESE	9.72
41-60	136	23	270	SESE	9.72
41-60	137	11	270	SESE	9.72
41-60	138	16	200	SESE	9.72
41-60	139	18	210	SESE	9.72
41-60	140	19	208	SESE	9.72
41-60	141	34	263	PSME	12.64
41-60	142	42	68	SESE	12.64
41-60	143	26	290	SESE	12.64
41-60	144	39	38	LIDE	12.64
41-60	145	41	63	LIDE	12.64
41-60	146	33	90	LIDE	12.64
41-60	147	39	78	TSHE	12.64
41-60	148	37	63	LIDE	12.64
41-60	149	39	96	LIDE	12.64
41-60	150	39	56	LIDE	12.64
41-60	151	32	90	LIDE	12.64
41-60	152	24	260	TSHE	12.64
41-60	153	35	235	SESE	12.64
41-60	154	37	245	LIDE	12.64
41-60	155	40	245	LIDE	12.64
41-60	156	34	346	SESE	12.64

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
41-60	157	24	265	SESE	12.64
41-60	158	23	170	LIDE	12.64
41-60	159	40	76	LIDE	12.64
41-60	160	52	131	TSHE	12.64
41-60	161	43	94	SESE	11.69
41-60	162	36	46	SESE	11.69
41-60	163	21	3	SESE	11.69
41-60	164	41	333	SESE	11.69
41-60	165	34	354	SESE	11.69
41-60	166	38	49	SESE	11.69
41-60	167	11	36	SESE	11.69
41-60	168	32	87	SESE	11.69
41-60	169	42	18	LIDE	11.69
41-60	170	41	55	SESE	11.69
41-60	171	33	104	SESE	11.69
41-60	172	29	106	SESE	11.69
41-60	173	25	324	SESE	11.69
41-60	174	39	47	SESE	11.69
41-60	175	31	50	SESE	11.69
41-60	176	23	39	SESE	11.69
41-60	177	26	83	SESE	11.69
41-60	178	34	81	SESE	11.69
41-60	179	36	54	ALRU	11.69
41-60	180	4	37	ALRU	11.69
81-100	181	16	82	SESE	1214.58
81-100	182	17	236	LIDE	1214.58
81-100	183	23	37	SESE	1214.58
81-100	184	22	52	SESE	1214.58
81-100	185	19	63	PSME	1214.58
81-100	186	28	230	SESE	1214.58
81-100	187	14	33	SESE	1214.58
81-100	188	11	13	SESE	1214.58
81-100	189	1	104	SESE	1214.58
81-100	190	28	17	LIDE	1214.58
81-100	191	30	7	ABGR	1214.58
81-100	192	22	209	SESE	1214.58
81-100	193	34	81	LIDE	1214.58
81-100	194	24	220	SESE	1214.58
81-100	195	17	351	ABGR	1214.58

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
81-100	196	13	103	LIDE	1214.58
81-100	197	18	3	ABGR	1214.58
81-100	198	15	263	SESE	1214.58
81-100	199	24	219	LIDE	1214.58
81-100	200	16	103	SESE	1214.58
81-100	201	29	357	LIDE	41.19
81-100	202	11	68	SESE	41.19
81-100	203	33	9	SESE	41.19
81-100	204	26	336	SESE	41.19
81-100	205	32	347	SESE	41.19
81-100	206	34	336	SESE	41.19
81-100	207	33	358	SESE	41.19
81-100	208	26	59	SESE	41.19
81-100	209	25	81	SESE	41.19
81-100	210	27	344	PSME	41.19
81-100	211	34	149	LIDE	41.19
81-100	212	52	351	SESE	41.19
81-100	213	37	2	SESE	41.19
81-100	214	53	154	SESE	41.19
81-100	215	45	183	SESE	41.19
81-100	216	34	345	SESE	41.19
81-100	217	47	147	SESE	41.19
81-100	218	39	357	SESE	41.19
81-100	219	44	131	LIDE	41.19
81-100	220	51	118	LIDE	41.19
81-100	221	6	290	SESE	14.93
81-100	222	4	270	SESE	14.93
81-100	223	15	205	SESE	14.93
81-100	224	20	250	SESE	14.93
81-100	225	17	195	SESE	14.93
81-100	226	29	200	SESE	14.93
81-100	227	24	200	SESE	14.93
81-100	228	5	268	SESE	14.93
81-100	229	8	250	SESE	14.93
81-100	230	5	340	PIMU	14.93
81-100	231	3	88	SESE	14.93
81-100	232	8	269	SESE	14.93
81-100	233	5	260	SESE	14.93
81-100	234	4	300	SESE	14.93

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
81-100	235	30	200	SESE	14.93
81-100	236	19	120	SESE	14.93
81-100	237	27	232	SESE	14.93
81-100	238	24	220	SESE	14.93
81-100	239	12	190	PSME	14.93
81-100	240	12	200	SESE	14.93
100+	241	27	283	TSHE	12.89
100+	242	40	310	LIDE	12.89
100+	243	35	260	SESE	12.89
100+	244	22	234	LIDE	12.89
100+	245	29	255	SESE	12.89
100+	246	28	284	LIDE	12.89
100+	247	46	270	LIDE	12.89
100+	248	17	40	UMCA	12.89
100+	249	14	10	SESE	12.89
100+	250	3	30	SESE	12.89
100+	251	26	357	SESE	12.89
100+	252	11	315	SESE	12.89
100+	253	18	315	SESE	12.89
100+	254	33	92	SESE	12.89
100+	255	1	16	SESE	12.89
100+	256	5	31	SESE	12.89
100+	257	22	84	SESE	12.89
100+	258	42	235	LIDE	12.89
100+	259	35	288	SESE	12.89
100+	260	21	312	LIDE	12.89
100+	261	29	225	LIDE	18.23
100+	262	4	295	SESE	18.23
100+	263	11	296	SESE	18.23
100+	264	11	273	SESE	18.23
100+	265	39	280	SESE	18.23
100+	266	19	252	LIDE	18.23
100+	267	43	250	SESE	18.23
100+	268	36	213	LIDE	18.23
100+	269	39	266	LIDE	18.23
100+	270	25	92	LIDE	18.23
100+	271	10	230	SESE	18.23
100+	272	24	268	SESE	18.23
100+	273	8	210	ALRU	18.23

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
100+	274	16	255	SESE	18.23
100+	275	11	265	ALRU	18.23
100+	276	9	295	SESE	18.23
100+	277	31	205	LIDE	18.23
100+	278	18	273	LIDE	18.23
100+	279	28	286	LIDE	18.23
100+	280	25	210	ALRU	18.23
100+	281	20	217	SESE	67.94
100+	282	22	3	SESE	67.94
100+	283	32	225	SESE	67.94
100+	284	16	62	SESE	67.94
100+	285	21	68	PSME	67.94
100+	286	28	36	SESE	67.94
100+	287	13	155	PSME	67.94
100+	288	28	182	LIDE	67.94
100+	289	33	86	LIDE	67.94
100+	290	4	235	SESE	67.94
100+	291	21	293	LIDE	67.94
100+	292	20	328	TSHE	67.94
100+	293	11	235	SESE	67.94
100+	294	18	186	SESE	67.94
100+	295	11	146	SESE	67.94
100+	296	19	168	LIDE	67.94
100+	297	38	74	SESE	67.94
100+	298	11	225	SESE	67.94
100+	299	6	269	SESE	67.94
100+	300	3	232	SESE	67.94
HW OG	301	6	38	SESE	341.96
HW OG	302	2	30	SESE	341.96
HW OG	303	0	0	SESE	341.96
HW OG	304	1	335	SESE	341.96
HW OG	305	10	320	SESE	341.96
HW OG	306	6	308	SESE	341.96
HW OG	307	2	310	SESE	341.96
HW OG	308	1	350	SESE	341.96
HW OG	309	0	0	SESE	341.96
HW OG	310	0	0	SESE	341.96
HW OG	311	1	355	SESE	341.96
HW OG	312	4	360	SESE	341.96

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
HW OG	313	3	18	SESE	341.96
HW OG	314	1	345	SESE	341.96
HW OG	315	0	0	SESE	341.96
HW OG	316	1	18	SESE	341.96
HW OG	317	3	18	SESE	341.96
HW OG	318	4	348	SESE	341.96
HW OG	319	2	240	SESE	341.96
HW OG	320	2	235	SESE	341.96
MW OG	321	4	9	SESE	462.15
MW OG	322	0	0	SESE	462.15
MW OG	323	1	6	SESE	462.15
MW OG	324	1	351	SESE	462.15
MW OG	325	4	335	SESE	462.15
MW OG	326	0	0	SESE	462.15
MW OG	327	2	3	SESE	462.15
MW OG	328	2	337	SESE	462.15
MW OG	329	0	0	SESE	462.15
MW OG	330	1	134	SESE	462.15
MW OG	331	1	292	SESE	462.15
MW OG	332	3	297	SESE	462.15
MW OG	333	1	331	SESE	462.15
MW OG	334	0	0	SESE	462.15
MW OG	335	1	334	SESE	462.15
MW OG	336	2	331	SESE	462.15
MW OG	337	4	297	SESE	462.15
MW OG	338	0	293	SESE	462.15
MW OG	339	0	298	SESE	462.15
MW OG	340	295	78	SESE	462.15
RRPOG	341	23	278	SESE	4.78
RRPOG	342	19	251	SESE	4.78
RRPOG	343	28	249	SESE	4.78
RRPOG	344	2	273	SESE	4.78
RRPOG	345	13	327	SESE	4.78
RRPOG	346	34	323	SESE	4.78
RRPOG	347	2	331	TSHE	4.78
RRPOG	348	23	355	SESE	4.78
RRPOG	349	27	242	SESE	4.78
RRPOG	350	27	310	SESE	4.78
RRPOG	351	20	255	SESE	4.78

<b>Age Class</b>	<b>Plot Number</b>	<b>Slope</b>	<b>Aspect</b>	<b>Dominant Canopy Species</b>	<b>Site Area (Hectare)</b>
RRP OG	352	13	260	SESE	4.78
RRP OG	353	14	207	SESE	4.78
RRP OG	354	23	225	SESE	4.78
RRP OG	355	3	315	TSHE	4.78
RRP OG	356	35	347	PSME	4.78
RRP OG	357	21	344	PSME	4.78
RRP OG	358	12	357	SESE	4.78
RRP OG	359	32	323	SESE	4.78
RRP OG	360	34	340	SESE	4.78



## Appendix B. Species list

*Species found in at least 10% of the plots sampled:*

<b>Species (Scientific Name)</b>	<b>Species (Common Name)</b>	<b>Age Class Species Found</b>
<i>Abies grandis</i>	Grand Fir	All age classes
<i>Achlys triphylla</i>	Vanilla Leaf	All classes except 81-100
<i>Actaea rubra</i>	Baneberry	All age classes
<i>Arbutus menziesii</i>	Pacific Madrone	All classes except 41-60
<i>Asarum caudatum</i>	Wild Ginger	All age classes
<i>Athyrium filix-femina</i> var. <i>cyclosorum</i>	Lady Fern	All age classes
<i>Berberis nervosa</i>	Oregon Grape	All age classes
<i>Calypso bulbosa</i>	Fairy Slipper	All age classes
<i>Campanula prenanthoides</i>	California Harebell	All age classes
<i>Cardamine californica</i>	Toothwort	All age classes
<i>Clintonia andrewsiana</i>	Red Clintonia	All age classes
<i>Disporum hookeri</i>	Hooker's Fairy Bells	All age classes
<i>Dryopteris arguta</i>	Coastal Wood Fern	All classes except 100+
<i>Galium triflorum</i>	Sweet Scented Bedstraw	All age classes
<i>Gaultheria shallon</i>	Salal	All age classes
<i>Lithocarpus densiflorus</i>	Tanbark Oak	All age classes
<i>Lonicera hispidula</i> var. <i>vacillans</i>	Hairy Honeysuckle	All age classes
<i>Lotus stipularis</i>	Stipulate Lotus	All age classes
<i>Oxalis oregana</i>	Redwood Sorrel	All age classes

Species found in at least 10% of the plots sampled (continued):

Species (Scientific Name)	Species (Common Name)	Age Class Species Found
<i>Pentagramma triangularis</i>	Goldenback Fern	All age classes
<i>Polystichum munitum</i>	Western Sword Fern	All age classes
<i>Pseudotsuga menziesii</i> var. <i>menziesii</i>	Douglas-fir	All age classes
<i>Pteridium aquilinum</i> var. <i>pubescens</i>	Bracken Fern	All age classes
<i>Rhododendron macrophyllum</i>	Rhododendron	All age classes
<i>Rubus parviflorus</i> var. <i>velutinus</i>	Thimbleberry	All classes except OG
<i>Rubus ursinus</i>	California Blackberry	All age classes
<i>Sequoia sempervirens</i>	Coast Redwood	All age classes
<i>Stachys bullata</i>	Hedge Nettle	All classes except 81-100
<i>Tiarella trifoliata</i> var. <i>unifoliata</i>	Sugar Scoop	All age classes
<i>Toxicodendron diversilobum</i>	Poison Oak	All age classes
<i>Trientalis latifolia</i>	Starflower	All age classes
<i>Trillium ovatum</i>	Western Wake Robin	All ages classes
<i>Tsuga heterophylla</i>	Western Hemlock	All age classes
<i>Umbellularia californica</i>	California Bay	All age classes
<i>Vaccinium ovatum</i>	Huckleberry	All age classes
<i>Vaccinium parvifolium</i>	Billberry	All age classes
<i>Vancouveria planipetala</i>	Inside Out Flower	All age classes
<i>Viola sempervirens</i>	Redwood Violet	All ages classes

*Species found in at least 5% of the plots sampled:*

Species (Scientific Name)	Species (Common Name)	Age Class Species Found
<i>Adenocaulon bicolor</i>	Trail Plant	All age classes
<i>Adiantum aleuticum</i>	Five-Finger Fern	All age classes
<i>Alnus rubra</i>	Red Alder	All classes except OG
<i>Archtostryphos columbiana</i>	Columbia Manzanita	0-20, 21-40
<i>Blechnum spicant</i>	Deer Fern	All classes except 0-20
<i>Ceanothus thyrsiflorus</i>	Wild Lilac	0-20, 21-40, 41-60, 100+
<i>Chimaphila menziesii</i>	Little Prince's Pine	All age classes
<i>Corallorhiza maculata</i>	Spotted Coral Root	41-60, 81-100, 100+, OG
<i>Epilobium angustifolium</i> var. <i>circumvagum</i>	Fireweed	0-20, 21-40, 41-60
<i>Myrica californica</i>	Wax Myrtle	All classes except 100+
<i>Rhamnus alnifolia</i>	Alder-Leaved Coffeeberry	0-20, 21-40, 81-100, OG
<i>Ribes menziesii</i>	Canyon Gooseberry	0-20, 21-40, 81-100, OG
<i>Rosa gymnocarpo</i>	Wood Rose	All age classes
<i>Rubus leucodermis</i>	Blackcap Raspberry	0-20, 21-40, 41-60, OG
<i>Smilacina racemosa</i>	False Solomon Seal (Fat)	All age classes
<i>Smilacina stellata</i>	False Solomon Seal (Slim)	All age classes
<i>Trillium chlorpetalum</i>	Giant Wake Robin	0-20, 81-100, OG
<i>Viola glabella</i>	Stream Violet	81-100, 100+, OG
<i>Whipplea modesta</i>	Modesty	All age classes

*Species found in less than 5% of the plots sampled:*

<b>Species (Scientific Name)</b>	<b>Species (Common Name)</b>	<b>Age Class Species Found</b>
<i>Agoseris retrorsa</i>	Spearleaf Agoseris	0-20, 21-40
<i>Anaphalis margaritacea</i>	Pearly Everlasting	0-20, 21-40
<i>Aquilegia formosa</i>	Northwest Crimson Columbine	0-20, 41-60, OG
<i>Aralia californica</i>	Elk Clover	81-100, OG
<i>Baccharis pilularis</i>	Coyote Bush	0-20, 21-40
<i>Berberis aquifolium</i>	Holly-Leaved Barberry	81-100, OG
<i>Yabea microcarpa</i>	California Hedge Parsley	0-20, 21-40
<i>Chenopodium berlandieri</i>	Pitseed Goosefoot	0-20
<i>Chlorogalum pomeridianum</i>	Soap Plant	0-20, 41-60
<i>Claytonia perfoliata</i>	Miner's Lettuce	21-40, 41-60
<i>Claytonia sibirica</i>	Candyflower	All classes except OG
<i>Collomia heterophylla</i>	Variableleaf Collima	0-20, 21-40
<i>Convolvulus occidentalis</i>	Morning Glory	21-40
<i>Corallorhiza striata</i>	Striped Coral Root	41-60, 81-100, 100+
<i>Cordylanthus tenuis</i>	Slender Bird's Beak	0-20
<i>Cornus canadensis</i>	Bunchberry	81-100
<i>Corylus cornuta</i> var. <i>californica</i>	Hazelnut	0-20, 21-40, OG
<i>Cynoglossum grande</i>	Hound's Tongue	0-20, 21-40, 41-60. 81-100
<i>Dicentra formosa</i>	Western Bleeding Heart	0-20, 21-10, 41-60, 100+

*Species found in less than 5% of the plots sampled (continued):*

<b>Species (Scientific Name)</b>	<b>Species (Common Name)</b>	<b>Age Class Species Found</b>
<i>Epilobum siliatum</i>	Northern Willow Herb	0-20, 41-60
<i>Equisetum arvense</i>	Horsetail Fern	All age classes
<i>Fragaria vesca</i>	California Strawberry	0-20, 41-60
<i>Galium californicum</i>	California Bedstraw	0-20, 21-40, OG
<i>Goodyera oblongifolia</i>	Rattlesnake Plantain	41-60, 81-100, OG
<i>Hemizonia corymbosa</i>	Tarweed	41-60
<i>Holodiscus discolor</i>	Oceanspray	0-20
<i>Iris douglasiana</i>	Douglas Iris	All classes except 0-20
<i>Lathyrus vestitus</i>	Common Pacific Pea	0-20, 41-60, OG
<i>Lepechinia calycina</i>	Pitcher Sage	100+
<i>Lithophragma glabrum</i>	Bulbous Woodland Star	21-40
<i>Lotus purshianus</i> var. <i>purshianus</i>	Lotus	100+
<i>Mimulus aurantiacus</i>	Sticky Monkey Flower	0-20
<i>Nemophila menziesii</i>	Baby Blue Eyes	0-20
<i>Nemophila parviflora</i>	Small-Flowered Nemophila	0-20, 41-60
<i>Phacelia bolanderi</i>	Bolander's Phacelia	0-20, 41-60, 81-100
<i>Pinus muricata</i>	Bishop Pine	41-60, 81-100, 100+, OG
<i>Pinus sabiniana</i>	Gray Pine	100+
<i>Polygala californica</i>	Milkwort	0-20, 41-60, 81-100, OG
<i>Polypodium californicum</i>	Leather Fern	21-40, 81-100, OG

*Species found in less than 5% of the plots sampled (continued):*

<b>Species (Scientific Name)</b>	<b>Species (Common Name)</b>	<b>Age Class Species Found</b>
<i>Prunella vulgaris</i>	Heal-All, Self-Heal	21-40
<i>Pyrola picta</i>	Whiteveined Wintergreen	0-20
<i>Salix lasiolepis</i>	Arroyo Willow	0-20
<i>Salix scouleriana</i>	Scouler Willow	0-20, 100+
<i>Sambucus racemosa</i>	Coast Red Elderberry	100+
<i>Sanicula crassicaulis</i>	Pacific Sanicle	0-20, 41-60, 81-100
<i>Satureja douglasii</i>	Yerba Buena	0-20, 21-40, 41-60
<i>Scoliopus bigelovii</i>	Fetid Adder's Tongue	81-100
<i>Scrophularia californica</i>	California Bee Plant	0-20, 21-40
<i>Stachys ajugoides</i> var. <i>rigida</i>	Emerson's Hedge Nettle	81-100, OG
<i>Stellaria crispa</i>	Curled Starwort	0-20
<i>Stephanomeria exigua</i>	Wirelettuce	21-40
<i>Symphoricarpos albus</i> var. <i>laevigatus</i>	Snowberry	41-60, 100+
<i>Taxus brevifolia</i>	Pacific Yew	0-20, 100+
<i>Torreya californica</i>	California Nutmeg	0-20, 21-40
<i>Petasites frigidus</i>	Coltsfoot	0-20
<i>Urtica dioica</i>	Stinging Nettle	100+
<i>Veratrum californicum</i> var. <i>californicum</i>	Corn Lily	81-100, OG
<i>Vicia americana</i> var. <i>americana</i>	American Vetch	0-20
<i>Woodwardia fimbriata</i>	Giant Chain Fern	81-100, OG

*Exotic species:*

<b>Species (Scientific Name)</b>	<b>Species (Common Name)</b>	<b>Age Class Species Found</b>
<i>Arabidopsis thaliana</i>	Moose Ear Cress	0-20, 21-40, 41-60
<i>Cirsium vulgare</i>	Common Bull Thistle	0-20, 21-40, 41-60
<i>Cortaderia selloana</i>	Pampas Grass	0-20, 21-40, 41-60
<i>Genista monspessulana</i>	French Broom	0-20
<i>Hypochaeris glabra</i>	Smooth Cat's Ear	0-20, 21-40, 41-60
<i>Hypochaeris radicata</i>	Rough Cat's Ear	41-60
<i>Lactuca saligna</i>	Willowleaf Lettuce	0-20
<i>Leontodon taraxacoides</i>	White-Flowered Hawk Bit	0-20, 21-40
<i>Rorippa sylvestris</i>	Creeping Yellow Cress	0-20
<i>Senecio bigelovii</i>	Ragwort	21-40
<i>Sonchus asper</i>	Spiny Sow Thistle	0-20, 21-40
<i>Stellaria media</i>	Common Chickweed	21-40
<i>Taraxacum officinale</i>	Common Dandelion	0-20

*Old-growth species:*

<b>Species (Scientific Name)</b>	<b>Species (Common Name)</b>	<b>Age Class Species Found</b>
<i>Anemone deltoidea</i>	Windflower	Old-growth
<i>Euonymus occidentalis</i>	Western Burning Bush	Old-growth
<i>Rhamnus purshiana</i>	Cascara Buckthorn	Old-growth
<i>Rubus spectabilis</i> var. <i>franciscanus</i>	Salmonberry	Old-growth

## Appendix C. Summary of concluding results

### *Stand parameters and specific tree species:*

Total Tree Density	Linear decrease, Lower in OG	41-60 years
Tree Shannon-Weiner Diversity Index	Bimodal (s-curve). Lower in OG	41-60 years
Tree Species Richness	Bimodal (s-curve), Lower in OG	41-60 years
<i>Sequoia sempervirens</i> Importance	Linear increase, Higher in OG	41-60 years
<i>Tsuga heterophylla</i> Importance	Linear increase, Higher in OG	41-60 years
<i>Tsuga heterophylla</i> Dominance	Linear increase, Lower in OG	41-60 years
<i>Pseudotsuga menziesii</i> var. <i>menziesii</i> Dominance	Bimodal (convex), Lower in OG	41-60 years
<i>Lithocarpus densiflorus</i> Dominance	Bimodal (concave), Lower in OG	41-60 years
<i>Lithocarpus densiflorus</i> Importance	Bimodal (concave), Lower in OG	41-60 years
Canopy Cover	Bimodal (convex), Higher in OG	81-100 years
Total Species Richness	Bimodal (concave), Lower in OG	81-100 years
Total Tree Dominance	Linear increase, Higher in OG	81-100 years
<i>Sequoia sempervirens</i> Dominance	Linear increase, Higher in OG	81-100 years
<i>Alnus rubra</i> Importance	Linear increase, Lower in OG	81-100 years
<i>Umbellularia californica</i> Importance	Bimodal (concave), Higher in OG	100+ years
<i>Abies grandis</i> Importance	Bimodal (convex), Lower in OG	100+ years



*Understory parameters and specific understory species:*

All Exotic Species Cover	Linear decrease, Lower in OG	41-60 years
Exotic Species Cover	Linear decrease, Lower in OG	41-60 years
Herbaceous Cover	Bimodal (concave), Higher in OG	41-60 years
<i>Viola sempervirens</i> Cover	Bimodal (convex), Higher in OG	41-60 years
Understory Cover	Bimodal (concave), Higher in OG	81-100 years
Understory Richness	Bimodal (concave), Lower in OG	81-100 years
<i>Trillium ovatum</i> Cover	Linear increase, Higher in OG	81-100 years
<i>Clintonia andrewsiana</i> Cover	Linear increase, Higher in OG	81-100 years
<i>Gaultheria shallon</i> Cover	Linear increase, Higher in OG	81-100 years
<i>Rhododendron macrophyllum</i> Cover	Bimodal (concave), Higher in OG	81-100 years
<i>Toxicodendron diversilobum</i> Cover	Bimodal (concave), Higher in OG	81-100 years
Understory Shannon-Weiner Diversity Index	Bimodal (convex), Lower in OG	100+ years
Understory Evenness	Bimodal (convex), Lower in OG	100+ years
<i>Oxalis oregana</i> Cover	Bimodal (concave), Higher in OG	100+ years
<i>Tiarella trifoliata</i> var. <i>unifoliata</i> Cover	Linear increase, Higher in OG	100+ years